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An Assessment of the Competitive Ability of Oak Species in the Central Hardwood Region Using both Pre-Harvest Treatment Data and Stem Analysis Techniques

Robert William Edward Quackenbush
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**PURDUE UNIVERSITY
GRADUATE SCHOOL
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By Robert Quackenbush

Entitled

An Assessment of the Competitive Ability of Oak Species in the Central Hardwood Region Using both Pre-Harvest Treatment Data and Stem Analysis Techniques

For the degree of Master of Science

Is approved by the final examining committee:

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6/30/2016

Date

AN ASSESSMENT OF THE COMPETITIVE ABILITY OF OAK SPECIES IN THE
CENTRAL HARDWOOD REGION USING BOTH PRE-HARVEST TREATMENT
DATA AND STEM ANALYSIS TECHNIQUES

A Thesis

Submitted to the Faculty

of

Purdue University

by

Robert William Edward Quackenbush

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

August 2016

Purdue University

West Lafayette, Indiana

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ABSTRACT

Quackenbush, Robert W. M.S., Purdue University, August 2016. An Assessment of the Competitive Ability of Oak Species in the Central Hardwood Region Using both Pre-Harvest Treatment Data and Stem Analysis Techniques. Major Professor: Dr. Michael Jenkins.

The density of advance regeneration of oak species has been in decline across the Central Hardwood Region (CHR) for the past 50 years. This phenomenon has been accredited to many different factors, ranging from predation and browse by wildlife, to human induced changes in the environment which include massive clearcutting, land use change from forest to agriculture, and suppression of fires which played an intricate role in the development of oak systems across the CHR. The objectives of this research project were to compare densities of oak advance regeneration across two different environmental gradients within the CHR, in particular the mesic uplands of south central Indiana in the Hoosier National Forest and the xeric uplands of the Missouri Ozarks located within the Sinkin Experimental Forest. In addition, we compared the development of white oak species versus their competitors following a disturbance (clearcutting) up until the stem exclusion stage of forest development. We used a mixture of ordination and regression techniques to evaluate our objectives. Our findings suggest that the distribution of red oak species advance regeneration is correlated with xeric sites

that exhibit convex topography in Missouri. Environmental variables in Indiana were limited in their range and likely were the reason we did not detect any environmental trends in advance regeneration within Indiana. When considering environmental influences on white oak development following a clearcut in Indiana we did not detect any significance in terms of the likelihood of a white oak achieving a higher canopy position over its two nearest competitors. Studies of this nature are important for the continued development and prorogation of oak forests across the CHR.

CHAPTER 1. INTRODUCTION

1.1 Review of Oak Management Literature

Oak species (*Quercus* spp.) have long dominated the forest landscape of the Central Hardwood Region. At the end of the glacial period a large portion of the Central Hardwood Region was covered in spruce/pine boreal forest. Approximately 6,000- 9,000 years ago this forest cover was replaced by a mix of pine and oak hardwood forest, which retained dominance into the Holocene Epoch (Loftis and McGee 1993). However, over the past few decades many researchers have noticed a decline in the abundance of oak species, especially in the regeneration layer. Studies from the 1950's illustrated the fact that oak species abundance was beginning to decline, especially on mesic sites and areas lacking disturbance (Weitzman and Trimble 1957, Carvell and Tryon 1961). Additional research brought to light the role that vegetative competition, deer browse, and land use practices played in the decline of oak abundance across the Central Hardwoods Region (Pallardy et al. 1988; Lorimer et al. 1994; Abrams 2003). Today, in the absence of active management, successful oak recruitment is occurring only on more xeric sites across the region (Abrams and Nowacki, 1992). In general, it is reported that self-perpetuating oak systems occur most often where site indices are 60 or less (Johnson et al. 2009), while indices greater than 60 support greater competition from more mesic species such as black cherry (*Prunus serotina*), blackgum (*Nyssa sylvatica*), maple species (*Acer* spp.)

and tuliptree (*Liriodendron tulipifera*) (Loftis and McGee 1993). On more mesic sites, a shift in composition is occurring, and this change is attributed to changes in climate and disturbance regimes resulting from human population growth (Dey 2002).

Early use of fire by Native Americans served to perpetuate oak species across the landscape (Abrams 1992). During the post settlement era (1750-1930), fire continued to be used commonly to clear land for farming, and create conditions favorable for livestock grazing and wildlife (Loftis and McGee 1993). Oak species are well adapted to fire, as well as drought, which produces the conditions that facilitate fire. In particular, acorns that germinate below ground are insulated by the soil from fire's heat thus, increasing the probability that the root collar, with its abundance of vegetative buds, will survive low intensity surface fires. Furthermore, oak seedlings possess the ability to sprout rapidly in response to shoot kill from fire, and their ability to do so increases exponentially with increasing root mass; and oaks maintain a high root: shoot ratio which provides them with increased carbohydrate storage to aid in recovery from stressful conditions (Johnson et al. 2009).

Dominance of oak species in the presettlement era was promoted by a regime of periodic fire, but oak's dominance was also facilitated by the clearing of large tracts of forest for agriculture on lands that were later abandoned and allowed to grow back into forest. Also, extensive forested areas dominated by oak species were harvested, thus creating high intensity light environments that favored oak recruitment from the pool of large advance regeneration and stump sprouts. Reoccurring fires over time, associated with the large buildup of fuels from slash, reduced competing species in the understory and midstory layers, allowing for oak recruitment into the midstory during extended fire

free periods. This recruitment was favored by the growth strategy of oak species during early stand development. Oaks exhibit a growth strategy known as recurrent shoot dieback (Johnson et al. 2009) in which allocation of photosynthate is preferentially allocated to root growth regardless of the environment, but there is a minimum level of light needed for growth to occur, which varies among the oak species.

After the late 1930's, fire suppression all but removed fire from the disturbance regime of most eastern forests (Dey 2002). In response to this change, contemporary forest succession shifted composition away from shade-intolerant species (including oak species) and towards shade-tolerant species such as sugar and red maple (Abrams 1998, Brose and Van Lear 1998). In the absence of frequent fire, forest stocking increased, dense understories of shade tolerant trees and shrubs developed, and advance oak regeneration failed to develop due to low light conditions (Dey 2002). Shade from the competing understory vegetation is thought to be more detrimental to oak survival in early stand development than shading from the overstory (Lorimer et al. 1994). Competition from other vegetation, along with deer browsing, defoliation, and erratic seed production, are all factors that have contributed to oak regeneration failures (Loftis and McGee 1993, Abrams 2003). This failure poses a threat to both the economic and ecological sustainability of oak forests. Oak species are a high-value hardwood species, and thus are an important commodity. From a wildlife perspective, hard mast from oaks is a critical food resource for many animal species (McShea et al. 2007). Wildlife such as deer, squirrels, and turkeys utilize oak acorns in the fall and early winter to build up fat stores to provide enough reserve energy to endure the winter.

Today, oak management is still a primary concern of researchers and forest management agencies. Different even-aged harvesting techniques have been developed to promote oak regeneration, but these techniques vary in their effectiveness across the Central Hardwood Region. In the eastern Appalachians, a region high in vegetation diversity, oak management focuses on using varying shelterwood techniques to manipulate light conditions in the understory, with the objective of releasing oak species while still suppressing competing vegetation (Loftis 1990, Brose et al. 1999). In the western portion of the Central Hardwood Region, clearcutting remains an economically viable regeneration method for oak species (Roach and Gingrich 1968, Sander and Clark 1971). The goal of our research was to determine how advance regeneration of oak and competing species are distributed across topographic gradients in two parts of the Central Hardwood Region that differ in productivity. We also modeled how forest stands in the Hoosier National Forest vertically stratified approximately 30 years after being clearcut, building on the previous work of Swaim (2013) and Swaim et al. (2016).

In chapter 2 we evaluated how environmental differences between mesic and xeric upland oak forests of Indiana and Missouri influence the relative density and distribution of advance regeneration. Chapter 3, is a study of how white oak species vertically stratified during 23 years after clearcutting in southern Indiana, and we identified height growth thresholds associated with oak dominance in young even-aged stands. We concluded this research with a synthesis of successful oak management across the Central Hardwoods Region, with an emphasis on which silvicultural methods would work best to sustain oak on mesic upland sites on the Hoosier National Forest compared to those that work best on upland xeric sites in the Ozark Region in southeastern Missouri.

CHAPTER 2. A COMPARISON OF PRE-HARVEST OAK DENSITIES BETWEEN INDIANA AND MISSOURI

2.1 Abstract

The dwindling density of oak advance regeneration over the past 50 years has been a concern in forest management across the Central Hardwood Region. Various even-aged techniques have been used over the years to help ameliorate this issue, but more research is needed to resolve inconsistencies reported on oak regeneration success for given regeneration methods that are likely related to important environmental gradients that occur across the Central Hardwood Region. This study compared pre-harvest data across environmental gradients at two sites with differing productivity, Missouri (low productivity) and Indiana (high productivity). Relationships between the density of advance regeneration and environmental variables were examined by species group using regression techniques and non-metric multidimensional scaling analysis. Missouri had significantly greater densities of advance regeneration of red oak group species, while Indiana had significantly greater densities of advance regeneration of white oak group species. In a combined NMS analysis, plots in Missouri and Indiana were separated along gradients correlated with aspect and terrain shape index, although these differences were likely influenced by the limited range of both variables found at the Indiana site. Ordinations of individual sites revealed that the distribution of oak species was correlated

with more xeric conditions in Missouri, but no strong environmental gradients were identified in Indiana. Regression analyses revealed generally weak relationships between advance regeneration density and environmental and site variables. The density of black oak stems < 0.6 m tall displayed the strongest relationship to environmental variables (adjusted $R^2 = 0.364$, $p < 0.001$) of all oak species with greater density occurring in Missouri on more xeric convex slopes.

2.2 Introduction

The persistence of oak species (*Quercus*) during early stand development depends largely on the accumulation of advance regeneration under the dominant canopy and sub-canopy layers of a forest (Larsen and Johnson 1998). Therefore, contemporary forestry practices now consider the composition of the regeneration layer and relative size of oak reproduction when developing silvicultural prescriptions to sustain oak forests.

Commercial clearcutting, where all stems above a specified lower diameter are cut, was the common method of harvesting and regenerating oak forests during the 1960s through the 1980s. On more xeric sites in the Central Hardwood Region, where site indices for oaks are 60 or lower, clearcutting remains a viable option (Johnson et al. 2009).

However, on more mesic sites, different techniques are required to reduce competition from shade tolerant species before regeneration harvesting, and early successional species that tend to dominate following harvesting. During the 1950-60s, several studies in the Lake States and Appalachian Mountains examined the use of clearcutting on more mesic sites (Heiligmann et al. 1985, Beck and Hooper 1986, Hix and Lorimer 1991) and identified similar trends. Whereas the pre-harvest composition included a large oak component in the overstory, composition in post-harvest stands was dominated by red

maple (*Acer rubrum*), black cherry (*Prunus serotina*), tuliptree (*Liriodendron tulipifera*), and birch (*Betula* spp.).

These shifts in post-harvest composition have led researchers to develop new management techniques to promote oak advance regeneration in order to retain some component of oak stocking in future forests. One such silvicultural practice is the shelterwood system, an even-aged regeneration method. Under even-aged management, individual stands within a forest are comprised of overstory trees from the same age cohort, but the forest as a whole will consist of multiple stands that are of various ages (Johnson et al. 2009). Clearcutting is also a type of even-aged management, but on more mesic sites within the Central Hardwood Region clearcuts create a high intensity light environment that favors early successional species growth in the regeneration layer. Therefore, clearcutting is less able to regenerate oak species (Abrams and Nowacki 1992, Jenkins and Parker 1998). A more effective approach, the shelterwood method, treats the overstory and midstory in a series of harvests to promote oak development in the understory, and therefore build adequate populations of large oak advance regeneration. The technique requires an adequate source of advance oak regeneration in the understory, which may be a natural seed source of seedlings established by artificial means by planting or direct seeding. The exact density of advance oak regeneration required varies depending on site conditions, competitive intensity, seedling size, and management intensity. Reported ranges of adequate density of oak advance regeneration vary from 160-1600 stems/hectare (Clark and Watt, 1971) to 400-4,000 stems/hectare (Johnson et al. 2009). If adequate oak advance regeneration exists, the midstory and a large portion of the overstory is removed to allow additional growing space for the oak seedlings, but

enough shade is left to limit the growth of competing early-seral species that have higher light requirements. Once oak reproduction grows into the midstory, it is eventually released in a final removal cut, which consists of harvesting the remaining overstory trees. In situations where oak advance regeneration is limiting, establishment and preparatory cuts may be needed as a means to facilitate oak seedling establishment and growth by directly removing competitors in the understory. The key to a successful shelterwood treatment lies in obtaining an adequate amount of oak advance regeneration and growing it to competitive sizes before final release by overstory harvesting. Currently, competing vegetation must be controlled throughout the process and even perhaps after final overstory harvesting. Specific details of the shelterwood method will vary depending on site quality, levels of deer browsing and invasive species in areas where they are problematic.

Even-aged management techniques, such as shelterwood harvests, are a viable means to facilitate regeneration of oaks in many instances. However, understanding how environmental gradients that occur across the Central Hardwood Region affect oak establishment and survival is critical in insuring adequate advance regeneration of oak species. While oak species are able to reproduce and persist on xeric sites, they are much less successful on mesic sites due to competition from other species. Environmental variables such as slope steepness, slope position, and aspect are known to have an effect on soil moisture, nutrient availability, and light in forest communities (Hutchinson et al. 1999) and collectively they often produce xeric conditions that favor many oak species (Rochow 1972, Pallardy et al. 1988). Oak species have been shown to have a particular

association with xeric environments because of their ability to tolerate drought, and the reduced competition from mesophytic species on these sites.

Within the Central Hardwood Region there exists a gradient of site quality and productivity extending from the highly productive forests of the eastern Appalachian Mountains to the less productive forests of the Ozark Mountains in Missouri and Arkansas. A review of numerous studies conducted by Collins and Carson (2004) synthesized information across the environmental gradients of the Central Hardwood region to determine how oak distribution has been affected over the last 50 years. In particular, this study examined aspect, slope position, site index, soil moisture, stand age, and elevation as potential influences on the density of seedling, juvenile, and adult white oak, northern red oak, and chestnut oak. In Pennsylvania and Missouri, juvenile northern red oaks occurred in greater abundances on south-southeastern aspects (Zimmerman and Wagner 1979, Steiner et al. 1993), while another study found a greater abundance of mature and juvenile northern red oak stems on north and west-facing slopes in southern Pennsylvania (Keever 1973). In North Carolina, density of northern red oak juveniles did not differ with aspect (Keever 1953), and in Ohio the distribution of adult northern red oak showed no significant correlation with aspect (McCarthy et al. 1984). White oak showed higher reproduction densities on south facing slopes in North Carolina, while chestnut oak seedlings displayed higher densities on north facing slopes (Keever 1953).

With regard to slope position, saplings of both northern red and white oak had higher densities on upper slopes and ridgetops in central Missouri (Rochow 1972). While there is less information on the distribution of chestnut oak reproduction, mature trees were most abundant on upper slopes and ridgetop positions in New Jersey and North Carolina

(Whittaker 1956, Buell et al. 1966, and Lorimer 1980). Considering site index as an environmental variable revealed that northern red oak sapling abundance was associated with lower site indexes in Pennsylvania (Steiner et al. 1993), and increased survival with higher site indexes in North Carolina (Bourdeau 1954). In summary, studies of this nature are important in understanding the abundance of oak species reproduction across the environmental gradients in the Central Hardwood Region, especially because studies such as these are critical to the successful application of shelterwood management across the Region. However, when considered en masse these studies illustrate how the distribution of oak species across topographic gradients varies across the Central Hardwood Region.

The aim of this study was to further elucidate how topography influences the abundance of oak species in the regeneration layer, as this information may help direct future forest management. For this study, we compared the density of oak species in the regeneration layer across topographic gradients at two sites of differing productivity. Specifically, we compared pre-treatment data from the Regional Oak Study (ROS) in the Missouri Ozarks, a xeric upland site, with data from the Hoosier National Forest, an area of comparatively mesic sites located in south central Indiana. According to Spetich et al. (1999), potential productivity at the Indiana site is 5.5 m³/ha/year vs. 3.5 m³/ha/year at the Missouri site. We used pre-harvest data from the Indiana and Missouri sites to examine how advance regeneration varies across environmental gradients. In this study we addressed three questions:

- 1) How does the distribution of oak species vary across topographic gradients at two sites with differing productivity?

- 2) How does density of stems at the two sites vary by species across diameter classes?
- 3) How does the density of advance regeneration vary with topographic variables; does this relationship differ between the two sites of differing productivity?

2.3 Methods

2.3.1 *Study sites*

Data for this study were collected from oak-dominated forests in two states, Missouri and Indiana, and was provided by the USDA Forest Service.

Missouri

Data from Missouri were collected in 2009, from plots located within the Sinkin Experimental Forest which is located in southeast Dent County, Missouri. This area is located within the Current River Hills Subsection of the Ozark Highlands (Nigh and Schroeder 2002). Topography is characterized by steep slopes and narrow ridges. Soils in the area contain large portions of rock fragments and are dry and acidic. Parent material is derived from sandstone and dolomite layers of the Gasconade and Roubidoux formations.

Forests within these sites are 80-100 years old, and are fully-stocked with a mixture of scarlet oak (*Q. coccinea*), black oak (*Q. velutina*), white oak (*Q. alba*), and post oak (*Q. stellata*). While oaks dominate on most sites (70% of stand BA), forests also contain a mix of shortleaf pine, hickory species, flowering dogwood, red maple, sassafras, and blackgum. Site index values range from 19 to 23 meters (black oak base age 50 years).

Understory reproduction varies from oak species on lower quality sites to predominately non-oak species on high quality sites.

Data were collected within 20 rectangular units (each 5 ha in size) that were established parallel to the slope contour. Data were collected for overstory, midstory, and regeneration layers using concentrically nested circular plots. Each unit consisted of 6 evenly spaced 0.05-ha (12.62 m radius) overstory circular plots ($n=120$) in which live stems ≥ 25 cm DBH were measured by species. Midstory trees (live stems ≥ 5 cm but < 25 cm DBH) were measured by species within a 0.01 ha plot (5.6 m radius) and regeneration (stems < 5 cm DBH) was measured by species within a 0.004 ha (3.57 m radius) plot originating 8 m from plot center at a bearing of 45° . Regeneration was tallied into five height classes: 1) < 0.3 m, 2) $0.3 - 0.6$ m, 3) $> 0.6 - 0.9$ m, 4) $> 0.9 - 1.2$ m, 5) > 1.2 m. Environmental variables measured included percent slope, aspect, terrain shape index (McNab, 1989), and hill slope position (backslope, footslope, and shoulder).

Indiana

Data from Indiana were collected in 2010, from two sites located in the unglaciated southern part of the state, within the Tell City ranger district of the Hoosier National Forest. These sites were located within the Crawford Upland, Mitchell Karst Plain, and Escarpment sections of the Shawnee Hills Natural Region (Homoya et al. 1985). The parent material is derived from Pennsylvanian and Mississippian bedrock. The physiography of the region is characterized by sandstone outcroppings that form cliffs at higher elevations, with lower elevations containing more limestone and limestone derived soils (Homoya et al. 1985). Forests in the area are roughly 100 years old, and composition varies with the topography. Dry and dry-mesic sites are dominated by oak

and hickory species, with blackjack and post oak species occurring on the most xeric of sites. More mesic sites are characterized by a beech-maple component, with ironwood and sugar maple common in the understory. Site index for this area was estimated to be 23 meters (black oak at base age 50 years).

Each site was approximately 40 hectares and was compartmentalized into 9 units, with three plots placed in each unit for a total of 54 plots between both sites. Data were collected using a series of concentrically nested circular plots. Overstory data were collected within a 0.05 hectare (12.62 m radius) plot, where all live stems greater than 11.4 cm DBH were measured by species. The midstory was sampled within a 0.02 hectare (7.98 m radius) subplot where all live stems greater than 3.8 cm but less than 11.4 cm DBH were measured by species. Regeneration data were collected within a 0.004 hectare (3.57 m radius) subplot located 6.1 meters at a 45° from plot center. All living stems ≤ 3.8 cm DBH were tallied by height into five classes: 1) < 0.3 m tall, 2) $\geq 0.3 - 0.6$ m tall, 3) $\geq 0.6 - 0.9$ m tall, 4) $\geq 0.9 - 1.37$ m tall, 5) ≥ 1.37 m tall.

2.3.2 *Data Preparation and Analyses*

Stem density data were compiled into five cm diameter classes by species to create diameter frequency distributions. Densities of advanced regeneration were summarized in a way that consolidated size differences into two generalized size classes, 1) 0-0.6 m tall and 2) > 0.6 m tall, where the first group reflects trees that will likely die from competition over time, and the second group reflects trees that have a higher probability of persistence over time. For all diameter frequency distributions and comparison of advanced regeneration, individual species data were combined into the following groups:

white oaks, red oaks, other overstory, understory, maples, and pine. The white oak group consisted of white oak (*Quercus alba*), post oak (*Quercus stellata*), chestnut oak (*Quercus prinus*), and chinkapin oak (*Quercus muehlenbergii*). The red oak group consisted of black oak (*Quercus velutina*), blackjack oak (*Quercus marilandica*), northern red oak (*Quercus rubra*), and scarlet oak (*Quercus coccinea*). The other overstory group included hickories (*Carya* spp.), American beech (*Fagus grandifolia*), white ash (*Fraxinus americana*), blackgum (*Nyssa sylvatica*), black cherry (*Prunus serotina*), sassafras (*Sassafras albidum*), and red elm (*Ulmus rubra*). The understory species group consisted of flowering dogwood (*Cornus florida*), eastern redbud (*Cercis Canadensis*), eastern redcedar (*Juniperus virginiana*), ironwood (*Ostrya virginiana*), Carolina buckthorn (*Rhamnus caroliniana*), and winged elm (*Ulmus alata*). The maple group was composed of red maple (*Acer rubrum*) and sugar maple (*Acer saccharum*), and the pine group consisted of shortleaf pine (*Pinus echinata*). Density (stems ha⁻¹), relative density, and basal area (m²ha⁻¹) were calculated by species for three diameter classes 1) 0-5 cm DBH, 2) 5.01-25 cm DBH, 3) > 25 cm DBH. Terrain shape index (TSI) was calculated by using a handheld clinometer to measure the vertical angle of inclination to the plot boundary in eight directions around plot center. After averaging these values, a positive value would indicate that a plot's topography tend toward being upslope, while a negative value indicates a downward slope orientation (McNab, 1989). Aspect was transformed into a linear scale using Beers' transformation: ($A' = \sin(A + 45) + 1$), where A = aspect in degrees; Beers et al. 1966). When needed the value of 8.75 was added to TSI values to allow for necessary transformations.

Data analyses

Advance regeneration

Oak regeneration data were organized by species and group (red and white oak) into two height classes (< 0.6 m tall, and ≥ 0.6 m) and analyzed using a combination of multiple linear regression techniques (SPSS, IBM Corp. 2013). Independent variables were state (MO or IN), percent slope, terrain shape index (TSI), slope position, and aspect. Square root and natural log transformations of variables were used to normalize data distributions as needed. Plots of studentized residuals versus fitted values were used to assess the assumption of constant variance (Netter et al. 1996). Residual plots and standard techniques were used to evaluate influence of potential outliers (Netter et al. 1996). State and slope position (back, foot, and shoulder slope) were represented with dummy variables equal to $k-1$ classes. If a categorical variable was significant in the final model, than that category had a significantly different intercept term than the baseline condition, which is represented by the category that was omitted. Multiplying a categorical variable (value of 0 or 1) by the continuous variables was used to evaluate whether the slope term associated with the continuous variable was significant between categories (Chatterjee and Price, 1991). To reduce the full model (includes state, percent slope, aspect, slope position, TSI, and their respective interaction terms), a backwards stepwise regression procedure was used (SPSS, IBM Corp. 2013). Criteria for a variable to stay in the model was set at $P < 0.05$. All predictors in the final models were significant at $P < 0.05$. Variance inflation factors (VIF) were used to detect whether independent variables in the final models had strong linear associations. Models with mean VIFs considerably greater than 1 were considered to be significantly collinear

variables (Netter et al. 1996). Mean VIFs for all of our final models were very close to 1 (Table 3).

Differences in composition of advance regeneration were compared between Missouri and Indiana using Wilcoxon rank sum tests with $\alpha = 0.05$ to compare means for each species group. This particular test was chosen because the data were not normally distributed and therefore a non-parametric technique was more suitable.

Non-metric multidimensional scaling (NMS)

Non-metric multidimensional scaling was used to evaluate the distribution of woody species in two diameter classes, 1) ≥ 5 cm DBH and 2) 5-25 cm DBH, across topographic gradients. Trees larger than 25 cm DBH were left out of these analyses because their frequency was not as large as the smaller diameter stems, and this would have made comparisons more difficult to scale. Pearson's correlation analysis was used to examine the relationships between continuous variables (percent slope, TSI, and transformed aspect) and NMS axis scores. Categorical variables (state and slope position) were not directly used in the correlation analysis, but were used to graphically sort plots in ordination space.

NMS analyses were conducted for Missouri and Indiana separately, and a composite analysis of Missouri and Indiana combined was done using PC-Ord (McCune and Grace 2002). Initial data runs were computed in auto-pilot mode to determine the appropriate dimensionality of each data run. Once the appropriate dimensionality was determined, several full runs (without autopilot) were conducted to determine the solution with the lowest stress and instability. Final runs consisted of 250 iterations using both real and randomized data. We used Sorenson's index as our distance measure, and set the stability

criterion at 0.00001. Final solutions reported in this study were those displaying the lowest stress, lowest instability, and highest variance explained by the distance matrix. To better illustrate how the advance reproduction of tree species (0-5 cm DBH) is distributed along environmental gradients within each site, bubble plots were constructed for the two dominant oak species and two dominant competitor species based on their relative densities.

2.4 Results

A summary of species group diameters by 5 cm classes for Indiana revealed a slight spike in the density of white oak species ranging 25-40 cm DBH (Figure 1A). The distribution of stem diameters in Missouri revealed a strong reverse-J shaped distribution (Figure 1B). For both sites the majority of stems occurred in the 5-15 cm DBH range, but differed greatly in species composition. In Indiana, the majority of species occupying the smaller diameter classes were maples and understory species (ironwood in particular). In Missouri, these smaller diameter classes contained a larger portion of white oak group species than Indiana, with the majority of competition coming from stems of blackgum and flowering dogwood. Oak species were dominant in the larger diameter classes at both sites, with Indiana having considerably greater densities of white oak group species in diameter classes 25-50 cm DBH than Missouri. In contrast, Missouri had considerably greater densities of red oak group species not only in diameter classes ranging from 25-50 cm DBH, but also across the entire diameter range (Figure 1A and 1B).

The midstory (stems 5.01-25 cm DBH) in Missouri was comprised of mostly white oak (2.90 m² ha⁻¹ basal area, 193 stems per ha⁻¹), hickory species (2.23 m² ha⁻¹ basal area, 113 stems ha⁻¹), and blackgum (0.65 m² ha⁻¹ basal area, 103 stems ha⁻¹; Table 1). The density

of flowering dogwood stems 5- 25 cm DBH in Missouri was roughly equal to that of blackgum (102 stems ha^{-1}). In Indiana, the midstory consisted of mostly sugar maple (2.02 $\text{m}^2 \text{ha}^{-1}$ basal area, 342 stems ha^{-1}), with white oak displaying the next highest basal area (0.53 $\text{m}^2 \text{ha}^{-1}$), and ironwood the next highest density (55 stems ha^{-1}). Total midstory mean stem density in Missouri was 679 ± 4 stems ha^{-1} while mean basal area was $8.15 \pm 0.05 \text{ m}^2 \text{ha}^{-1}$. Indiana midstory mean density was 698 ± 9 stems ha^{-1} , with a mean basal area of $4.63 \pm 0.02 \text{ m}^2 \text{ha}^{-1}$.

Overstory species composition (stems > 25 cm DBH) in Missouri was dominated by shortleaf pine (6.90 $\text{m}^2 \text{ha}^{-1}$ basal area, 66 stems ha^{-1}), white oak (5.76 $\text{m}^2 \text{ha}^{-1}$ basal area, 67 stems ha^{-1}), and black oak (4.95 $\text{m}^2 \text{ha}^{-1}$), with smaller components of hickory species (2.23 $\text{m}^2 \text{ha}^{-1}$ basal area, 31 stems ha^{-1}), scarlet oak (1.74 $\text{m}^2 \text{ha}^{-1}$ basal area, 15 stems ha^{-1}), and northern red oak (1.60 $\text{m}^2 \text{ha}^{-1}$ basal area, 14 stems ha^{-1} ; Table 1). The overstory in Indiana was largely white oak (14.43 $\text{m}^2 \text{ha}^{-1}$ basal area, 109 stems ha^{-1}) with a smaller component of post oak (2.73 $\text{m}^2 \text{ha}^{-1}$ basal area, 28 stems ha^{-1}). Mean overstory basal area in Missouri was $26.36 \pm 0.18 \text{ m}^2 \text{ha}^{-1}$, with a mean stem density of 307 ± 2 stems ha^{-1} , and in Indiana mean overstory basal area was $21.11 \pm 0.55 \text{ m}^2 \text{ha}^{-1}$, with a mean stem density of 170 ± 4 stems ha^{-1} .

In Missouri, advance regeneration (stems 0-5 cm DBH) was composed of mostly other overstory species ($8,823 \pm 413$ stems ha^{-1}) and understory species ($6,230 \pm 496$ stems ha^{-1}), with smaller densities of red oak group species ($3,439 \pm 228$ stems ha^{-1}) and white oak group species ($1,805 \pm 214$ stems ha^{-1}) present. Advance regeneration in Indiana was predominately composed of other overstory species ($14,765 \pm 1425$ stems ha^{-1}), with relatively equal densities of white oak group species ($4,223 \pm 481$ stems ha^{-1}) and

understory species ($4,261 \pm 476$ stems ha^{-1}), followed by red oak group species ($2,359 \pm 401$ stems ha^{-1}) and maple species ($2,908 \pm 389$ stems ha^{-1}). Missouri had a significantly greater density of red oak species advance regeneration than Indiana, as well as significantly greater density of understory species advance regeneration (Figure 2). Indiana had significantly greater densities of white oak group species advance regeneration, other overstory species, and maple species than Missouri.

NMS Ordinations

Non-metric multidimensional scaling analysis of Missouri and Indiana data combined showed that aspect and TSI were the environmental variables most strongly related to the relative density of trees 0-5 cm DBH, and trees 5.01-25 cm DBH (Figure 3). The final stress score for the three dimensional solution for this analysis was 13.71, and a Monte Carlo permutation test revealed that extracted axes were stronger than expected by chance ($p = 0.004$). Axes 2 and 3 for the solution accounted for 83% (axis 2 $r^2 = 0.253$, axis 3 $r^2 = 0.585$) of the variation in the ordination. Among the three environmental variables assessed (Aspect, TSI, and percent slope) aspect was most strongly associated with axis 2 ($r^2 = 0.352$), and TSI was most strongly associated with axis 3 ($r^2 = 0.155$; Table 2). Environmental vectors revealed that Missouri plots covered a greater range of transformed aspect and TSI values than Indiana (Figure 3A). Species relative densities for both sites combined overlaid on NMS axes revealed that the relative densities of mid-size (5.01-25 cm DBH) northern red oak, scarlet oak, white oak, and black cherry were all associated with more mesic aspects that have concave topography (Figure 3 B). Red maple in both small and mid-size classes, as well as small northern red oak, black oak, and white oak stems were associated with more xeric aspects. Ironwood and sugar maple

of both small and mid-sizes, as well as mid-sized post oaks appeared to be associated with convex topography. Transformed aspect ranged from 0.001 to 1.438 in Indiana and from 0 to 2 in Missouri. TSI ranged from -8.75 to 0.625 in Indiana and from -4.875 to 19.75 in Missouri (Table 3)

NMS analysis for the Indiana data revealed no strong correlations between environmental variables and on the relative density of trees 0-25 cm DBH (Table 2, Figure 4A). The final stress score for the three dimensional solution for this analysis was 11.87, and a Monte Carlo permutation test revealed that extracted axes were stronger than expected by chance ($p = 0.004$). Axes 1 and 3 accounted for 79% (axis 1 $r^2 = 0.165$, axis 3 $r^2 = 0.630$) of the variation in ordination. Of the three environmental variables analyzed, percent slope was most strongly associated with axis 1 and 3 ($r^2 = 0.053$ and 0.016 respectively), and aspect was most strongly associated with axis 1 ($r^2 = 0.021$; Table 2) although all correlation coefficients were very low. Plots of relative density of species overlaid across NMS axes showed no clear pattern for four focal species, suggesting that environmental gradients were not influencing species distributions (Figure 5).

NMS analysis of Missouri only data showed that aspect was most strongly correlated with the distribution of plots and species (Figure 4B). The final stress score for the three dimensional solution for this analysis was 15.06, and a Monte Carlo permutation test revealed that extracted axes were stronger than expected by chance ($p = 0.004$). Axes 2 and 3 for the solution accounted for 76% (axis 2 $r^2 = 0.140$, axis 3 $r^2 = 0.620$) of the variation in ordination. Out of the three environmental variables used, aspect was most strongly associated with axis 3 ($r^2 = 0.335$), while axis 2 was not strongly correlated with any environmental variable (maximum $r^2 = 0.040$ for TSI; Table 2). Plot level data

overlaid on NMS axes revealed that mid-sized red elm and black walnut were associated with more mesic aspects, with the majority of remaining species showing an association with the dry-mesic portion of the gradient. Shortleaf pine appeared to have the strongest association with the most xeric aspects, with small sized scarlet oak, sassafras, and black oak occurring on less xeric aspects (Figure 4 B). In Missouri, black oak, white oak, and red maple displayed greater relative density on more xeric aspects (Figure 6). Hickory species displayed a more uniform distribution across plots and did not show a strong affinity for measured environmental gradients (Figure 6).

Advance regeneration density and environmental variables

Regression analyses revealed generally weak relationships between advance regeneration density and environmental and site variables (adjusted R^2 range = 0.049 to 0.364). Density of black oak stems <0.6 m tall offered the best fit (adjusted $R^2 = 0.364$, $p < 0.001$) of all species with greater density occurring in Missouri on more xeric convex slopes (Figure 7). Northern red oak stems <0.6 m height were associated with xeric aspects on landforms other than shoulder slopes (adjusted $R^2 = 0.146$, $p < 0.001$). Significantly more white oak stems occurred in Indiana than in Missouri (adjusted $R^2 = 0.146$, $p < 0.001$; Table 4).

Relationships between advance regeneration ≥ 0.6 m tall and environmental and site variables were generally weaker than those for stems <0.6 m tall (max adjusted $R^2 = 0.176$). Greater density of black oak stems in the larger height class occurred on more xeric aspects (adjusted $R^2 = 0.148$; $p < 0.001$). Greater density of northern red oak stems occurred on landforms other than shoulder slopes (adjusted $R^2 = 0.049$, $p = 0.002$).

Greater density of white oak stems ≥ 0.6 m tall was associated with steeper slopes (adjusted $R^2 = 0.068$, $p = 0.023$). Density of white oak group species (including white oak, post oak, and chestnut oak) in this height class was lower in Indiana and increased with decreasing transformed aspect (more xeric conditions).

2.5 Discussion

Composition of the advance regeneration layer for Indiana reflected the mesic shift in vegetation communities that has been widely observed over the last 50 years (Abrams 1998, Lorimer et al. 1994, Dey 2002). Maple was the dominant species occupying the smaller diameter size classes in Indiana. This dense layer of shade tolerant vegetation will likely require future management activities to promote oak species. However, the densities of advance regeneration of oaks observed on Indiana sites (white oak species group: 4,223 stems ha^{-1} , red oak species group: 2,359 stems ha^{-1}) fall above the 160-1600 stem ha^{-1} range specified by Clark and Watt (1971), and within the 400-4000 stem ha^{-1} range specified by Johnson et al. (2009). Densities of red and white oak group species observed at our sites were greater than those observed at sites from the northern portion of the Hoosier National Forest in Indiana at the time of harvest in 1988 (white oak species group: 791 stems ha^{-1} , red oak species group: 1,097 stems ha^{-1} ; Swaim et al. 2016). White oak was the dominant species in the larger diameter classes, which may be a viable reservoir for future oak recruitment, but only if additional care is taken to reduce competition from maple species within the 5-15 cm DBH size classes. Red oak group species displayed the lowest density of any group in the advance regeneration layer and were secondary to white oak in the larger diameter classes. The lack of red oak group species across larger diameter sizes (i.e. > 5 cm DBH), in conjunction with a high density

of maple species, could potentially lead to a loss of the red oak species group within the Indiana sites if more is not done to recruit these species into the overstory.

Overall, Missouri had higher densities of red oak group species (mostly consisting of black oak) than Indiana, and red oak group species were present in all diameter classes in Missouri. Composition of advance regeneration in the Missouri sites differed from that of Indiana in that there were more stems of red oak group species present (Missouri RO = 3,439 stems ha⁻¹, Indiana RO = 2,359 stems ha⁻¹), but understory species (primarily flowering dogwood) acted as a greater source of competition than in Indiana (Missouri understory species = 6,230 stems ha⁻¹, Indiana understory species = 4,261 stems ha⁻¹). Jenkins and Pallardy (1993) also observed high densities of flowering dogwood in the regeneration layer of Ozark forests, as well as high densities of white oak in the smaller diameter size classes. We observed a similar trend in our data, where white oak group species were considerably more abundant in size classes ranging from 5-20 cm DBH in Missouri than in Indiana.

The influence of environmental and site variables of species composition varied across and within state. In NMS analysis, we observed a clear separation of sites between Indiana and Missouri, with Missouri sites associated with more mesic aspects and concave slopes. However, the apparent importance of these environmental gradients is more likely an artifact of differences between the ranges of environmental variables sampled at study sites within the two states. The Missouri study contained a broader range of aspects and TSI values (Table 3). In particular, the Indiana sites contained no plots with a TSI value greater than 0.65. Consequently, higher TSI value (more concave landforms) are only associated with plots in Missouri. Generally, sites in Missouri are

less productive than those in Indiana (Spetich et al. 1999), due to an array of edaphic and topographic conditions in Missouri associated with poor growing conditions (Kabrick et al. 2008).

Aspect and shape of the terrain influenced the distribution of species and density of species in Missouri, but not Indiana. The distribution of oak species and red maple stems in Missouri were most associated with xeric aspects. Smaller white oak advanced regeneration (0-5 cm DBH) density was greater in Indiana, but displayed no strong environmental associations. However, density of white oak stems > 5 cm DBH was greater at the Missouri sites and was correlated with xeric conditions. Our results found that the highest density of black oak advance regeneration occurred on westerly aspects with convex topography (summit or shoulder). Similar results were found by Rochow (1972) and Keever (1973), who observed greater red oak abundances on north and west facing aspects and on upper slopes and ridgetops. Overall differences in the density of red oak species between Missouri and Indiana reflects a similar trend found by Steiner et al. (1993), where greater red oak sapling abundance was associated with lower site indexes.

The high density of competing species observed across all sites highlights the need to control competition when applying silvicultural prescriptions (Swaim et al. 2016). When considering how to apply shelterwood management techniques to productive sites in the Central Hardwood Region, our results suggest that mechanical or herbicide control (Loftis 1990, Lorimer et al. 1994) may be more effective than fire alone, due to the high densities of shade tolerant stems in the midstory, and the low densities of oak species in the smaller diameter classes. Prescribed burning at these sites doesn't seem feasible at this point, largely because of the density of shade tolerant vegetation occurring, which

could decrease the likelihood of successful ignitions (Arthur et al. 2012). However, if burning was used as a management tool, burns should occur in the spring or winter and be at a medium-low intensity, as those types of burns have been shown to have the greatest success in oak recruitment (Brose, 2010), while dormant low intensity fires are less effective in top killing stems 15-25 cm DBH (Arthur et al. 2012). Initial harvest entries in Indiana should focus primarily on removing competition from non-oak species in the 5-25 cm diameter class. After this preparatory cut, canopy reduction can be used to facilitate the growth of oak advance regeneration on site, with additional openings occurring 5-10 years later if needed. Once oak species have established as the new mid-story structure, overwood removal should occur in order to release oaks fully into the overstory. Prescribed fire is useful at this stage to favor oak if needed (Brose et al. 2013, 2014).

The Missouri sites would likely be more suitable for shelterwood management techniques that involve burning and herbicide treatments (Loftis, 1990; Brose et al. 1999), especially since it has a well-distributed abundance of oak stems across the different diameter classes. Initial efforts should focus on reducing competition from dogwood and blackgum in the 5.01-10 cm DBH class. In the Missouri Ozarks, Dey and Hartman (2005) showed that three to four low intensity dormant season prescribed fires over a ten year period significantly reduced survival of flowering dogwood and blackgum advance reproduction that was < 15 cm in basal diameter. On our Missouri sites, competition from other non-oak species drastically declined in larger (> 10 cm DBH) diameter classes, which is likely a result of the xeric environment. Harvest entries toward

the end of the management scheme should account for the lack of large white oak stems (≥ 30 cm DBH), by removing a greater proportion of large red oak group species stems.

In conclusion, pre-harvest data are an important consideration for directing future forest management practices. When considering oak species management across the Central Hardwood Region, there is a stark contrast between Missouri and Indiana. Xeric sites conditions favor oak species more in Missouri than Indiana. Future management entries into these systems should consider the current composition and abundance of oak species, and the primary sources of competition they face for the persistence of oak species in managed forests across the Central Hardwood Region.

2.6 Tables and figures

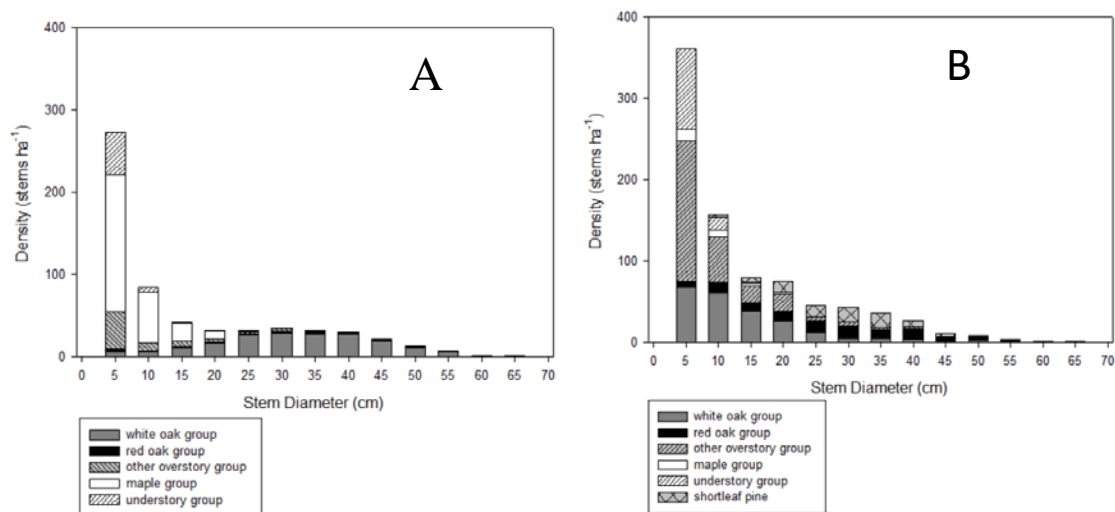


Figure 1. Diameter distribution of all live woody stems > 5 cm DBH at study sites for A) Indiana and B) Missouri, categorized by species groups into 5 cm diameter classes.

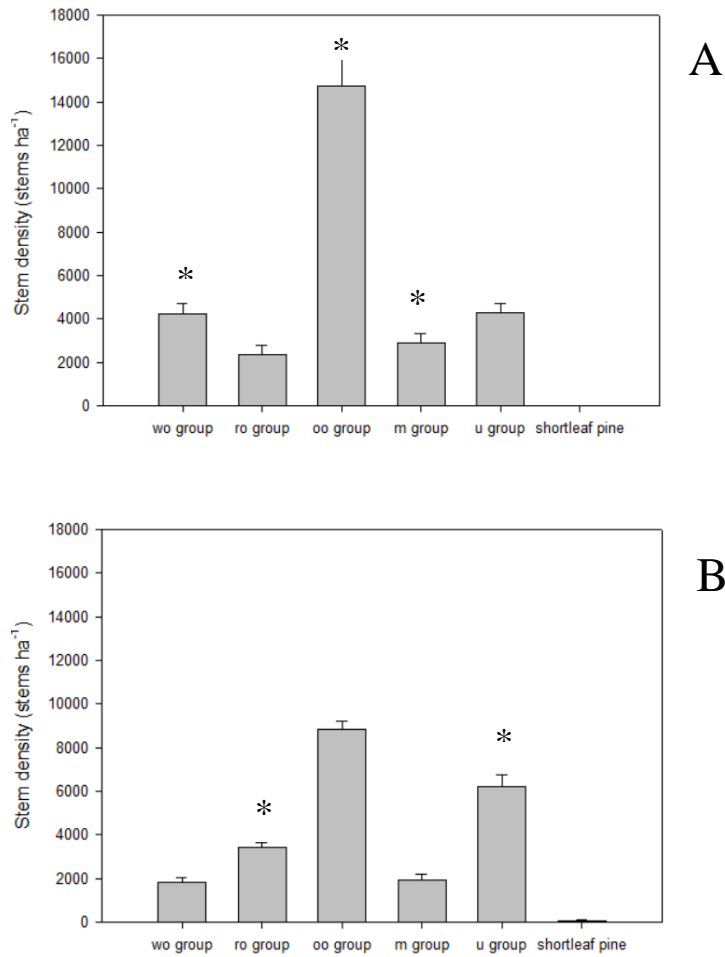


Figure 2. Advance regeneration (stems ≤ 5 cm DBH; mean ± 1 SE) density by species groupings at study sites for A) Indiana and B) Missouri. Asterisks indicate a significant difference ($P < 0.05$) in the density of a species group between sites. Significant differences were determined using a Wilcoxon rank sum test in Program R. Group labels are as follows: wo = white oak species, ro = red oak species, oo = other overstory species, m = maple species, and u = understory species.

Table 1. Basal area mean \pm 1SE ($\text{m}^2 \text{ha}^{-1}$) and density mean \pm 1SE (stems ha^{-1}) of all live trees > 5 cm DBH sorted into two diameter categories at study sites in Indiana and Missouri.

	Missouri stems (ha^{-1})		Missouri BA ($\text{m}^2 \text{ha}^{-1}$)		Indiana stems (ha^{-1})		Indiana BA ($\text{m}^2 \text{ha}^{-1}$)	
DBH (cm)	5.01-25	> 25	5.01-25	> 25	5.01-25	> 25	5.01-25	> 25
red maple	28 ± 7	6 ± 1	0.24 ± 0.08	0	38 ± 1	0	0.21 ± 0.09	0
sugar maple	3 ± 2	1 ± 1	0.04 ± 0.04	0	342 ± 1	2 ± 1	2.02 ± 0.22	0.12 ± 0.05
hickory	113 ± 12	31 ± 3	1.29 ± 0.18	2.23 ± 0.29	39 ± 1	4 ± 1	0.28 ± 0.07	0.43 ± 0.14
species								
eastern redbud	12 ± 4	2 ± 1	0.11 ± 0.06	0.11 ± 0.06	3 ± 1	0	0.01 ± 0.01	0
flowering dogwood	102 ± 12	20 ± 2	0.45 ± 0.06	0.45 ± 0.06	27 ± 1	0	0.08 ± 0.03	0
american beech	0	0	0	0	6 ± 1	0	0.02 ± 0.01	0
white ash	0	0	0	0	11 ± 1	0	0.12 ± 0.05	0
black walnut	8 ± 3	5 ± 1	0.18 ± 0.08	0.50 ± 0.13	0	0	0	0
blackgum	103 ± 12	22 ± 2	0.65 ± 0.10	0.82 ± 0.14	17 ± 1	0	0.11 ± 0.04	0.03 ± 0.03
ironwood	0	0	0	0	55 ± 1	0	0.19 ± 0.04	0
shortleaf pine	23 ± 6	66 ± 6	0.70 ± 0.17	6.90 ± 0.66	0	0	0	0
black cherry	4 ± 2	1 ± 1	0.05 ± 0.03	0.05 ± 0.03	3 ± 1	0	0.01 ± 0.01	0
white oak	193 ± 19	67 ± 5	2.90 ± 0.34	5.76 ± 0.46	44 ± 1	109 ± 1	0.53 ± 0.10	14.43 ± 1.21
scarlet oak	13 ± 4	15 ± 2	0.26 ± 0.09	1.74 ± 0.28	32 ± 1	4 ± 1	0	0.72 ± 0.23
chestnut oak	0	0	0	0	12 ± 1	8 ± 1	0.12 ± 0.05	0.92 ± 0.37
northern red oak	13 ± 3	14 ± 3	0.28 ± 0.09	1.60 ± 0.33	6 ± 1	3 ± 1	0.04 ± 0.03	0.41 ± 0.16
post oak	2 ± 1	1 ± 1	0.03 ± 0.02	0.13 ± 0.05	32 ± 1	28 ± 1	0.43 ± 0.11	2.73 ± 0.59
black oak	16 ± 4	44 ± 5	0.39 ± 0.11	4.95 ± 0.52	3 ± 1	5 ± 1	0.01 ± 0.01	0.72 ± 0.28
sassafras	11 ± 3	2 ± 1	0.12 ± 0.04	0.12 ± 0.04	19 ± 1	0	0.07 ± 0.03	0
red elm	34 ± 9	8 ± 2	0.49 ± 0.13	0.60 ± 0.15	2 ± 1	0	0.01 ± 0.00	0
Site mean total \pm SE	679 ± 4	307 ± 2	8.15 ± 0.05	26.36 ± 0.18	698 ± 9	170 ± 4	4.63 ± 0.02	21.11 ± 0.55

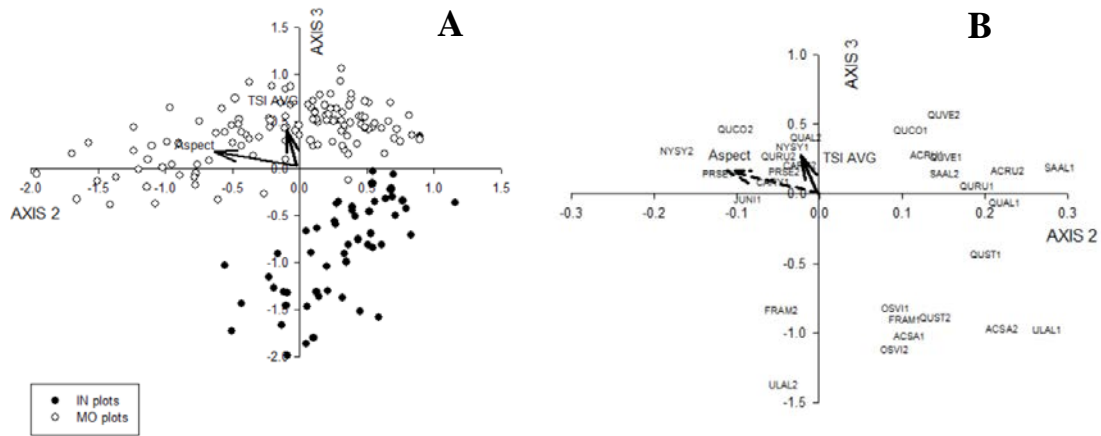


Figure 3. Results from a NMS run for both A) plot level and B) species level associations between the relative density of live woody stems (0-25 cm DBH) and environmental variables (aspect, TSI AVG, %slope) across Missouri and Indiana. Vector lines indicate the strongest environmental influence within the NMS run. Species abbreviations are separated by a 1 or a 2, which corresponds to their diameter range. Species values of 1 indicate a diameter range of 0-5 cm DBH, and a 2 indicates a diameter range of 5.01-25 cm DBH. Species abbreviations are as follows: ACRU = *Acer rubrum*, ACSA = *Acer saccharum*, CARY = *Carya spp.*, FRAM = *Fraxinus americana*, JUNI = *Juglans nigra*, LITU = *Liriodendron tulipifera*, NYSS = *Nyssa Sylvatica*, OSVI = *Ostrya virginiana*, PRSE = *Prunus serotina*, QUAL = *Quercus alba*, QUCO = *Quercus coccinea*, QURU = *Quercus rubra*, QUST = *Quercus stellata*, QUVE = *Quercus velutina*, SAAL = *Sassafras albidum*, ULAL = *Ulmus alata*.

Figure 4. Results from individual NMS runs comparing relative density of two diameter classes of live woody stems across environmental gradients for A) Indiana and B) Missouri. Species codes followed by a 1 refer to 0-5 cm DBH and a code of 2 refers to species 5.01-25 cm DBH. Vectors indicate the strongest environmental influence (cutoff set at $R = 0.200$).

Table 2. Pearson correlation coefficients of distance measures, NMS axis values, and environmental variables. Also included are the stress scores for the optimal solution for each data run.

Variance explained by axis		Axis 1	Axis 2	Axis 3
Allsites		R= 0.048	R= 0.253	R= 0.585
Missouri		R= 0.104	R= 0.140	R= 0.620
Indiana		R= 0.090	R= 0.276	R= 0.630

Correlations with environmental variables		Axis 1	Axis 2	Axis 3
Allsite				
Stress score	Aspect	R = 0.001	R= 0.352	R= 0.057
	TSI AVG	R= 0.000	R= 0.033	R= 0.155
	%slope	R= 0.001	R= 0.000	R= 0.001
	13.713			
Indiana				
Stress score	Aspect	R = 0.021	R= 0.001	R= 0.008
	TSI AVG	R = 0.002	R= 0.000	R= 0.016
	%slope	R= 0.053	R= 0.003	R= 0.016
	11.876			
Missouri				
Stress score	Aspect	R = 0.039	R= 0.002	R= 0.335
	TSI AVG	R = 0.022	R= 0.040	R= 0.008
	%slope	R = 0.021	R= 0.010	R= 0.002
	15.068			

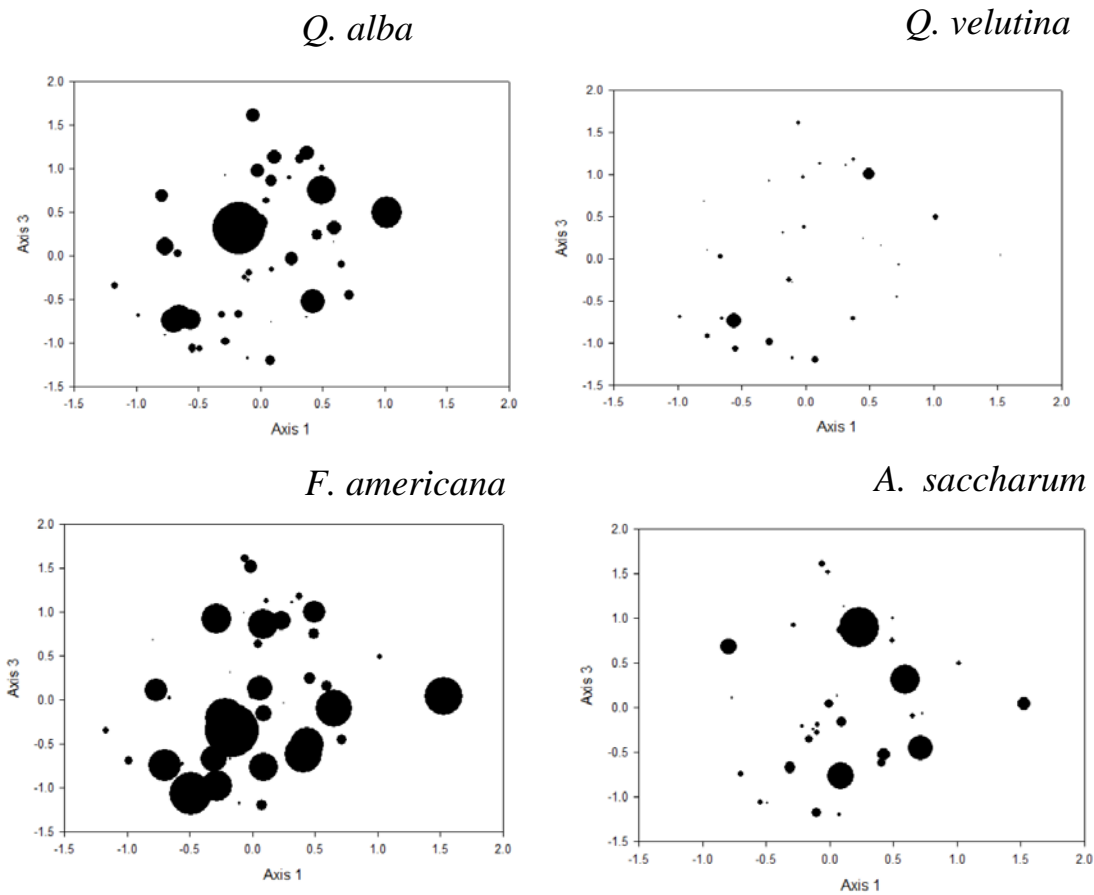


Figure 5. Bubble plots overlaid on NMS plot coordinates reflecting the relative density of *Quercus alba*, *Quercus velutina*, *Fraxinus americana*, and *Acer saccharum* within plots located in Indiana. Size of circles is proportional to the relative density of a particular species. All species shown consisted of live woody stems 0-5 cm DBH.

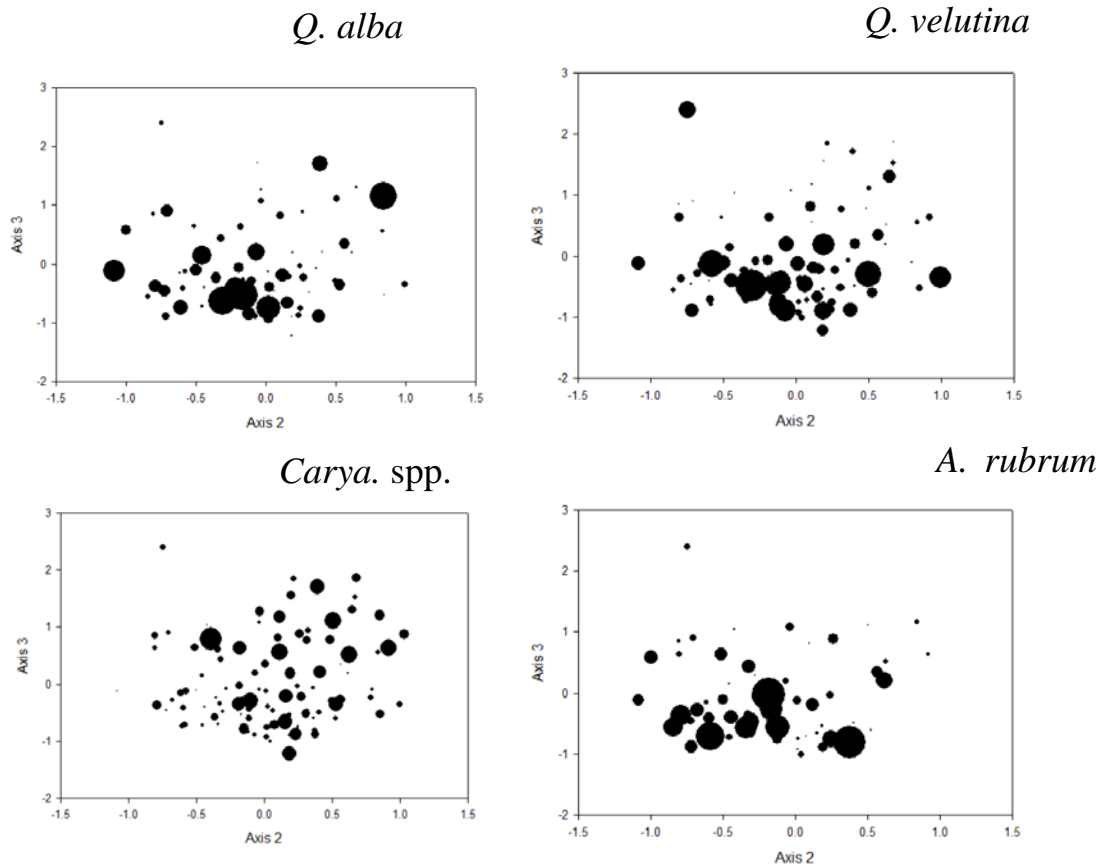


Figure 6. Bubble plots overlaid on NMS plot coordinates reflecting the relative density of *Quercus alba*, *Quercus velutina*, *Carya* spp., and *Acer rubrum* within plots located in Missouri. Size of circles is proportional to the relative density of a particular species. All species shown consisted of live stems 0-5 cm DBH.

Table 3. The range of environmental variables observed for Indiana and Missouri.

Indiana Sites			
	Beers' aspect	TSI	percent slope
mean	0.445	-3.199	28.370
SE	0.051	0.242	0.764
min	0.001	-8.75	18
max	1.438	0.625	42
Missouri Sites			
	Beers' aspect	TSI	percent slope
mean	1.096	0.993	26.392
SE	0.074	0.359	0.851
min	0	-4.875	3
max	2	19.75	50

Table 4. Final regression equations for two height classes of advance regeneration (stems ha^{-1}) from Missouri and Indiana versus aspect, slope position, slope percent, and terrain shape index.

Equation	F-statistic	Adj. R^2	VIF	P-Value
<u>Stems <0.6 m height</u>				
$\text{sqrt}(\text{ROG}) = 86.547 - 31.259 \text{ IN} - 7.036 \text{ sqrt}(\text{aspect}) - 6.914 \text{ sqrt}(\text{TSI} + 8.75)$	20.973	0.257	1.446	<0.001
$\text{sqrt}(\text{black oak}) = 86.361 - 34.360 \text{ IN} - 19.890 \text{ sqrt}(\text{aspect}) - 8.688 \text{ sqrt}(\text{TSI} + 8.75)$	34.051	0.364	1.379	<0.001
$\text{sqrt}(\text{northern red oak}) = 26.774 - 8.287 \text{ sqrt}(\text{aspect}) - 8.962 \text{ shoulder slope}$	9.986	0.095	1.051	0.001
$\text{sqrt}(\text{WOG}) = 31.211 + 25.481 \text{ IN}$	40.455	0.186	---	<0.001
$\text{sqrt}(\text{white oak}) = 30.305 + 22.544 \text{ IN}$	30.577	0.146	---	<0.001
<u>Stems ≥ 0.6 m height</u>				
$\ln(\text{ROG} + 1) = 3.385 - 0.597 \text{ sqrt}(\text{aspect})$	17.443	0.087	---	<0.001
$\ln(\text{black oak} + 1) = 3.521 - 2.278 \text{ sqrt}(\text{aspect})$	31.060	0.148	---	<0.001
$\ln(\text{northern red oak} + 1) = 1.440 - 1.214 \text{ SH}$	10.005	0.049	---	0.002
$\ln(\text{WOG} + 1) = 4.252 - 2.179 \text{ IN} - 0.892 \text{ sqrt}(\text{aspect})$	19.472	0.176	1.125	<0.001
$\ln(\text{white oak} + 1) = 5.453 + 0.26 \text{ slope}$	5.420	0.068	---	0.023

Categorical variables (1 if category, 0 if otherwise) were used for state (IN= Indiana and

MO= Missouri) and slope position (SH = shoulder slope, BS=backslope, FS= footslope).

To determine if individual slope terms were significant, categorical variables were multiplied by continuous variables and their significance in each regression was evaluated. All predictors in the final models were significant ($P < 0.05$). Average variance inflation factors (VIF) are provided for variables in multiple regression.

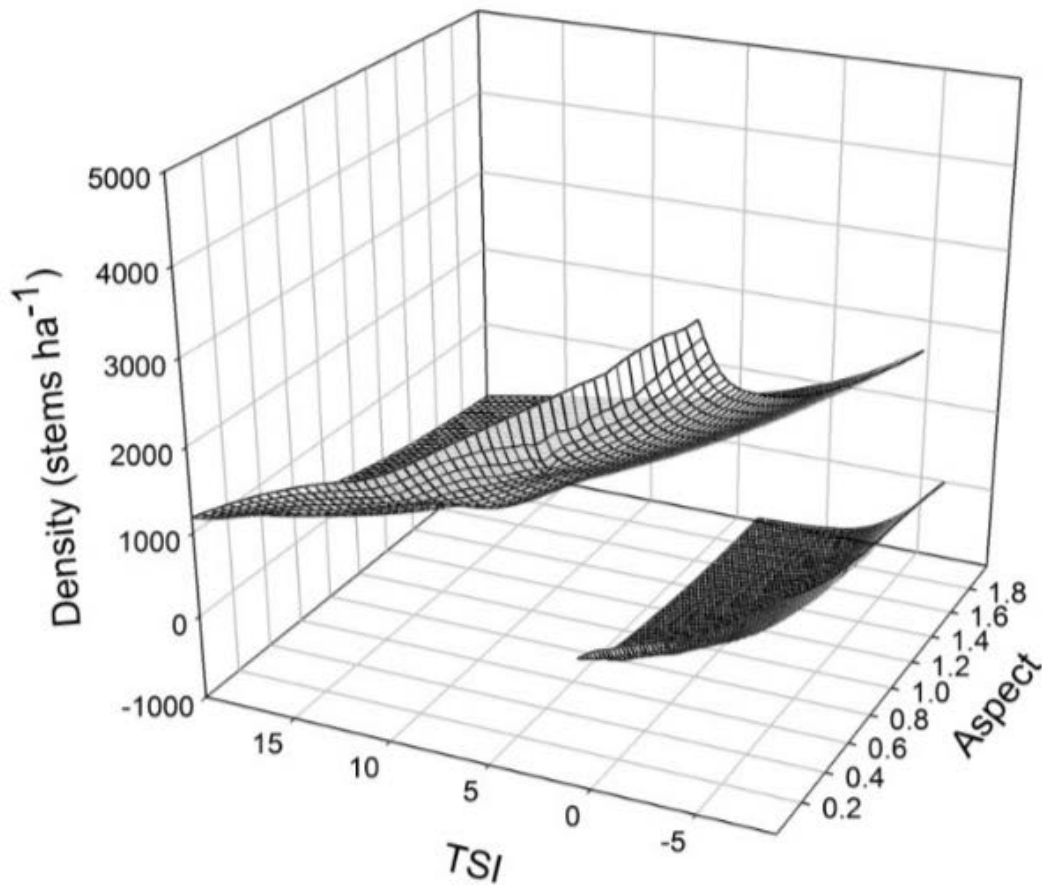


Figure 7. Density of black oak advance regeneration (stems ha⁻¹) as a function of TSI and aspect. Display was created by solving for the black oak equations in Table 6. Terrain shape index (TSI) was calculated using the protocol outlined in McNab, (1989). Aspect was transformed into a linear scale using Beers' transformation ($A' = \sin(A + 45) + 1$, where A = aspect in degrees; Beers et al. 1966)

CHAPTER 3. AN ASSESMENT OF WHITE OAK (*QUERCUS ALBA*) HEIGHT GROWTH FOLLOWING CLEARCUTTING IN HARDWOODS FORESTS OF SOUTHERN INDIANA

3.1 Abstract

Among members of the genus *Quercus*, white oak (*Q. alba*) is relatively long-lived, moderately tolerant of shade, drought tolerant, and is a highly valued timber and wildlife species. Understanding how this species establishes and persists over time within stands is important to tailoring silvicultural prescriptions to insure its continued presence in managed forests. To understand how white oak differentiates in height within developing stands following clearcutting, we destructively sampled 60 white oak stems of varying canopy positions along with the two nearest competitors (defined by intersecting crowns) for each white oak. Three cross sections were taken for each tree sampled, and annual rings were measured using a high-resolution bed scanner analyzed with the software WindendroTM. Height-age relationships were derived from published equations and canopy area was measured for each tree. Chi-squared tests at $\alpha = 0.05$ were used to evaluate if number of stems in dominant and co-dominant canopy position differed from expected by slope and aspect class. Crown area values were also compared across all three stands using one-way ANOVA ($\alpha = 0.05$) to evaluate differences with slope and aspect by species. The number of stems in the dominant and co-dominant classes in different slope-aspect classes did not differ from expected values and crown

area did not differ between slope-aspect classes. Across all stands, white oak stems lagged behind most other trees in height growth, with the exception of suppressed sugar maple (*Acer saccharum*) stems that were carried over from pre-harvest stands.

3.2 Introduction

Even-aged silvicultural techniques were the traditional method for regenerating oak species (*Quercus*) during the last fifty years. One of the most utilized and economical methods of even-aged management is clearcutting, a technique that involves removal of the dominant tree cover down to a specified diameter size in order to initiate regeneration (Johnson et al. 2009). In terms of oak management, clearcutting success is dependent upon having an adequate reservoir of oak regeneration present on the site prior to any type of removal (Roach and Gingrich 1968, Smith and Ashton 1993, Johnson et al. 2009), and the successful resprouting of oak stumps (Beck and Hopper 1986, Arthur et al. 1997). Therefore, clearcutting remains a viable option on the most xeric sites in the western portion of the Central Hardwood Region, as these forest sites are able to accumulate adequate amounts of oak advanced regeneration (Johnson et al. 2009).

In the central and eastern portions of the Central Hardwood Region, competition from other woody species increases dramatically as sites increase in quality. In some studies, the absence of adequate oak advance regeneration prior to clearcutting resulted in stands that contained little or no oak species in the developing stand, which shifted composition towards more shade tolerant (Hix and Lorimer 1991, Beck and Hooper 1986, Pallardy et al. 1988) or early successional species (Heiligmann et al. 1985, Sander and Clark 1971, Smith and Ashton 1993). Over the next 15 to 20 years, these woody species begin to differentiate and stratify vertically, eventually creating a new canopy layer that quickly

enters stem exclusion (Oliver and Larson 1996) and preventing establishment of new oak regeneration on the site. Therefore, if existing oak advance regeneration or stump sprouts are going to eventually recruit into the canopy of mature stands, they must be competitive with other species during early stages of stand development.

Forest stands stratify, or form multiple canopy layers, in a variety of patterns through a multitude of mechanisms. The composition and spatial mixture of species present can influence how a stand stratifies and the number of layers. At the species level, one of the most important factors contributing to stratification is species silvics, in particular shade tolerance, growth patterns, crown architecture, and successional role. Growth patterns of species vary accordingly, with early successional shade-intolerant species such as tuliptree (*Liriodendron tulipifera*), sweetgum (*Liquidambar styraciflua*) and red maple (*Acer rubrum*) exhibiting sustained growth patterns (Oliver and Larson 1996). This type of growth allows shoot elongation to occur as long as conditions in the environment remain favorable. Mid-tolerant and mid-successional species, such as oaks and hickories exhibit a preformed growth pattern, in which the amount of growth the species is capable of achieving is set during the previous growing season (Oliver and Larson 1996). Species that exhibit sustained growth do not have as large of a growth flush as species that exhibit preformed growth, but often time sustained growth allows a species to outgrow their preformed rivals, especially if favorable growing conditions persist for an extended period of time. These different growth patterns also influence the stiffness of lateral branches, with preformed growth species usually having stiffer lateral branches that provide protection for the terminal leader (Oliver and Larson 1996, Lockhart et al. 2006). These differences in stiffness could potentially be part of the reason that species such as

oaks are eventually able to outcompete their sustained growth competitors over the course of stand development, particularly toward the end of stem exclusion where crown abrasion begins to damage the terminals of subordinate trees, allowing upper canopy trees to maintain their dominance (Oliver and Larson 1996, Lockhart et al. 2006). When considering the shape of a crown, crown architecture has been shown to affect how cherrybark oak stratifies with sweetgum in east-central Mississippi. Work by Lockhart et al. (2006) demonstrated that the excurrent crown form of sweetgum allow enough light to penetrate the sub canopy to allow cherrybark oaks to eventually catch up and surpass them by age 23-25 years of stand development. Cherrybark oak has a decurrent growth form which allows it to maintain dominance once it reaches the upper canopy, because it reduces the light available because of its wider spreading crown.

Species height growth patterns vary considerably by region, and stratification does not occur evenly across a stand. In some instances, where resources are not limited, species that are initially suppressed early in stand development are able to achieve dominance and overtop their rivals (Oliver 1978, Larson 1986). Another factor influencing stratification is the difference in time of establishment. Hibbs (1983) showed that the oldest stems (those that established first) ended up being the tallest. Often, however, the tallest stems and shortest stems within a given stand are the same age (Oliver 1981, Smith and Ashton, 1993), so other factors must have determined the rate and likelihood of canopy ascension in these stands.

A species response to a single disturbance event, as well as the overall disturbance regime, are two additional mechanisms that may influence stratification. The frequency and severity of disturbances are known to alter species composition during secondary

succession, with frequent canopy disturbances shifting composition towards early successional species that are able to grow rapidly in response to environmental changes (Harper 1977, Oliver 1980) and creating a multi-aged stand. However, abiotic factors also play a role in determining which species establish in a stand and ultimately reach the canopy. For example, in a study assessing stratification of tree species following clearcutting in southern Indiana, Morrissey et al. (2008) observed that frequent droughts favored the survival and overstory recruitment of oaks species over more numerous tuliptree competitors.

In addition to the mixture of species present, the quality of the site, the spacing of species, and the different shade zones within the stand can all influence how stratification occurs. All species are influenced by site quality, with higher quality sites often increasing growth rates for all species present. Within a given site there can be variations in site quality. Sometimes these differences are extreme enough in their effect on species productivity that they can influence stand stratification, often favoring species that exhibit rapid shoot growth, or have the ability to tolerate stressful conditions. Examples from the literature include tuliptree outgrowing pines on productive sites, but not on sites that were considered poor quality (Doolittle 1958), as well as northern red oaks outgrowing red maple on mesic sites in the New England area, but not on very wet sites where red maple maintained dominance (Oliver et al. 1989, Oliver and Larson 1996). When considering spacing of species within a stand, at closer spacing those species that exhibit rapid early growth are often able to surpass and suppress slower growing species early on in stand development. When spacing between species is farther apart, the slower growing species are able to achieve greater height growth and can eventually surpass their competitors

(Cline and Lockard 1925, Oliver and Larson 1996). Examples of spacing effects on stratification include the cherrybark oaks (*Quercus pagoda*) and American sycamores (*Platanus occidentalis*), where cherrybark oak is able to compete with sycamore in instances where greater spacing occurs (Clatterbuck et al. 1987, Oliver 1989), as well as Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) which are able to compete with red alder when spaced farther apart (Stubblefield 1978, Stubblefield and Oliver 1978). Finally, shade zone within a stand can also influence stratification patterns within a stand. Trees that grow beneath the co-dominant canopy layer experience a zone of high shade which directly affects how the tree grows. Trees in this high shade zone begin to slow in height growth and alter their crown shape (Busgen and Bunch 1929, Meng 1986, Tucker et al. 1987, Oliver and Larson 1996).

Johnson et al. (2009) describes three ways in which oak species are able to maintain dominance during the stem exclusion stage. The first is through inherently faster growth, which allows the oaks to attain canopy dominance over some of their more slowly growing rivals. This has been demonstrated in post disturbance stands from New England to Kentucky where species of oak have been shown to grow at the same or faster than their shade tolerant competitors (Hibbs 1983, Arthur et al. 1997, Ward and Stephens 1999). Another way in which oaks may maintain dominance is with an initially superior crown position, which is often the case if a legacy component of oak overstory or midstory is left behind as a seed source for the new developing stand. The third way in which oaks maintain their dominance is through persistence (Johnson et al. 2009) or latent dominance (Zenner et al. 2012); both can be generally defined as the continued growth of oaks while their competitors do poorly under the same edaphic or

environmental conditions. For example, in cases such as droughts, a larger proportion of oak species will survive the drought than the faster growing red maple or tuliptree that may be present (Hill 1985, Morrissey et al. 2008, Johnson et al. 2009). In other instances, the origin of the oaks may confer an advantage across time; oaks that begin with large advanced root development from sprout origin have been shown to ascend into the upper canopy quicker and maintain dominance (Loftis 1990, Brose 2011, Zenner et al. 2012).

In order for oak species to successfully establish in the canopy in mixed species forests, they must be available to respond to disturbance events that favor their survival and growth over other species. In particular, drought and fire are known to facilitate oak species over their competitors in nutrient poor soils of xeric environments (Johnson et al. 2009, Kabrick et al. 2014). Density of advance regeneration of oak species in pre-disturbance stands has declined across the Central Hardwood Region for the last 50 years. Researchers have noted several reasons for this phenomenon, including fire suppression policies of the 1930's (Dey 2002), shade from competing understory vegetation (Lorimer et al. 1994), deer browse, and erratic seed production (Loftis and McGee 1993). However, even in cases when advance regeneration of oak species are present, individuals are often unable to ascend to the canopy in developing post-disturbance stands (Swaim et al. 2016). As a result, it is often sprout origin oaks that end up persisting in post-harvest stands (Roach and Gingrich 1968, Sander and Clark 1971, Smith and Ashton 1993, Swaim et al. 2016).

Prior to European settlement, white oak was a dominant species in the Central Hardwood Region, comprising between 24 and 81% of witness trees across the region (Abrams 2003). Today, white oak density across much of the Central Hardwood Region

has dwindled. Abrams (2003) attributed the decline of white oak in the eastern portion of the Central Hardwood Region to several factors: extensive logging, fire suppression, and chestnut blight. Extensive logging created high intensity light environments which likely favored more shade-intolerant oak species such as northern red oak (*Quercus rubra*) or black oak (*Q. velutina*). White oak was a valuable timber species in some areas during that time period, and in high demand, which only facilitated the dominance of other oak species (Whitney 1994, Whitney and DeCant 2001). The use of clearcutting and land clearance for farming facilitated the recruitment of other oak during the early 1900's (Abrams 2003, Dey 2014). With the loss of chestnut across portions of the region due to chestnut blight, and the removal of large areas of pines and white oaks through clearcutting, red oak species were able to expand their range across most of the eastern portion of the Central Hardwood Region (Crow 1988, Nowacki et al. 1990, Abrams 2003). The inability of white oak to sustain itself on more mesic sites requires additional research into the growth and development of this species in forest stands following management.

The aim of this study was to evaluate the relative canopy position of white oaks stems in three developing mixed-species stands 23 years after clearcutting. We examined how site characteristics, such as aspect and percent slope, influenced white oak height development and crown area in a competitive environment. We predict that white oaks will achieve a higher canopy position on xeric sites with steep topography, as these sites produce more stressful conditions (in terms of moisture availability) that should favor the more resilient white oak versus its more mesic competitors such as red maple or tuliptree.

3.3 Methods

3.3.1 Study Sites

Sites used in this study occurred within two adjoining natural regions of southern Indiana: the Highland Rim Natural Region, and the Shawnee Hills Natural Region (Homoya et al., 1985). These regions are unglaciated, with acidic silt loam soils that are derived from sandstone, loess, and siltstone parent material. Steep slope and narrow ridges are found within the Highland Rim, and broad ridgetops are found within the Shawnee Hills Region. Species composition on the Highland Rim upland areas was mostly oak species which included chestnut oak (*Quercus prinus*), while the Shawnee Hill region is dominated by black oak, white oak, and scarlet oak. More mesic ravines contain American beech (*Fagus grandifolia*), northern red oak, and maple species, with black walnut (*Juglans nigra*) and white ash (*Fraxinus americana*) also present. Of the three stands sampled, stand 3 was the largest (8.1 ha) followed by stand 4 (7.6 ha) and stand 5 (4.5 ha; Table 1).

3.3.2 Data Preparation and Analyses

A total 60 white oaks and 120 competitor trees were destructively sampled from stands that had white oak relative densities $\geq 1.5\%$. White oak stems were not randomly sampled, but instead were purposefully selected to include a range of canopy positions. We did not sample coppice white oak trees or obvious stump sprouts, but were otherwise unable to distinguish individuals originating as advance regeneration from stump sprouts. Two competitors were destructively sampled for each target white oak tree. A competitor was defined as a tree competing directly with the subject tree for resources, and

possessed a crown that touched or overtopped the crown of the target white. For each tree sampled, three cross sections were cut with a chainsaw at three heights: stump height (0.051 m), breast height (1.37 m), and at the base of the live crown (height varied). For each tree, we recorded the following measurements: DBH, crown length (longest axis), crown width (perpendicular to longest axis), canopy class (1 = suppressed, 2 = intermediate, 3 = co-dominant, and 4 = dominant), and height at base of live crown. The distance and azimuth from the target white oak to each competitor was also recorded.

Tree cross sections were sanded with 1,000 – 1,200 grit sandpaper to make rings more visible. Cross sections were then scanned between 800 to 1,200 dpi using a high-resolution flatbed scanner (Epson 10000XL). Once uploaded, the digital images were analyzed with the software WinDendroTM (Version 6.01, Regent Instruments Inc., Quebec, Canada). For each cross section analyzed, four radii were chosen (two based on the longest axis and two perpendicular to the longest axis), and the width of rings as well as the number of rings was determined for each radius. Data from each radius were then averaged per cross section. Cross section averages (ring width and ring count) were compiled across each section taken to create tree ring measurement series for each tree. Tree ring measurement series were imported into a growth-height estimator created in Microsoft Excel that employed equations derived from Cancino et al. (2013), which combined the methods of Carmean (1972) with those of Kariuki (2002) for estimating terminating heights of tree rings that disappear between cross sections. The Cancino et al. (2013) method was used because it creates a continuous time fraction and can be applied to any distance between cross sections along the stem, which was ideal for our study

since we only had 3 cross sections per tree. The combined equation as defined by Cancino et al. (2013) is as follows:

$$\Delta T_j C_T = 0.5 (\Delta T_j C + \Delta T_j T),$$

where 0.5 refers to the assumption that each cross section occurs in the middle of annual height growth, $\Delta T_j C = j - 0.5 / r_i - r_{i+1}$, where “j” is the number of the inner ring, and “r_i” is the number of growth rings in the ith cross section (Carmean’s equation [equation 2a]; Cancino et al. 2013), and $\Delta T_j T = w_j / w_{k+1}$ where “w_j” is the cumulative width of the respective growth rings, and “w_{k+1}” is the cumulated ring width up to the ring following the last ring lost in the cross section (TARG equation [equation 2c.]; Cancino et al. 2013).

The abundance of stems by canopy class was analyzed using chi-squared tests. Two separate 2 x 2 contingency tables were created to assess observed vs. expected stem abundance by canopy class and topography (aspect and slope percent). Canopy classes were combined into two groups: 1) suppressed and intermediate and 2) co-dominant and dominant. Each plot was treated as a separate case, and all cases were summarized by either aspect or percent slope. Of the potential 60 cases of white oaks vs. competitors there were 57 cases total used in the analyses due to the loss of 3 cases due to missing and broken cross sections associated with extended periods of storage.

Percent slope was divided into two groups: $\geq 8\%$ slope, $< 8\%$ slope. Aspect was converted from azimuth readings to a linear scale by using Beer’s transformation: $A' = A \cos (45-A)+1$ where A’ is the transformed aspect and A is the aspect measured in the field (Beers et al. 1966). This scale assigns the highest value of 2 to mesic NE aspect, and a value of 0 to the more xeric SW aspect. For this study, values ranging from 0-1 were categorized as xeric and values ranging from 1.01 -2 were categorized as mesic.

Crown areas of all destructively sampled trees were calculated by canopy class across all three stands. We compared these crown areas by classes for each aspect and slope class. Initial assessment of the data revealed a right skewed distribution, which resulted in the use of a log transformation to achieve a normal distribution. We tested the assumption of normality with a Shapiro-Wilks test for normality and a F test to compare variance. Classes used for slope were 1) $\geq 8\%$, and 2) $< 8\%$ slope. For aspect, 1) 0-1 and 2) 1.01-2 were used. A one-way ANOVA ($\alpha = 0.05$) using a generalized linear model compared models with a backwards stepwise procedure to determine which model, if any, showed a significant effect of slope or aspect on crown area.

3.4 Results

Of the 60 white oaks destructively sampled, 3% were in the suppressed canopy position, 50% occupied the intermediate canopy class, and 47% occupied the co-dominant class, with no white oaks present in the dominant canopy position. In terms of competition from other species, the most abundant nearest competitors were red maple, bigtooth aspen (*Populus grandidentata*), tuliptree, sassafras (*Sassafras albidum*), and sugar maple (Figure 1). Red maple species sampled occurred 100% of the time in the co-dominant canopy class. Tuliptree and bigtooth aspen occurred mostly in the co-dominant canopy position (92% and 75% respectively), with smaller portions occurring in the dominant canopy class (8% and 25% respectively). For sugar maple, 80 % of stems were in the intermediate canopy position, while only 20% occurred in the co-dominant canopy position. Sassafras trees that were sampled occurred 36% in the intermediate canopy position, and 64% in the co-dominant canopy position. Stem counts of species by canopy class in each stand revealed that the majority of all stems sampled were co-dominant in

canopy position, with sugar maple and ironwood occupying co-dominant positions in stand 3, and sugar maple, white ash, and sassafras occupying co-dominant positions in stand 4 (Table 1). Aspect varied between the three stands sampled, but mean percent slope was relatively similar across sites, with stand 5 exhibiting a narrower range of slope values (Table 2). Of the three stands that were sampled stand 4 had the highest mean tree height for all stems sampled (13.1 meters). Stand 3 had a mean tree height of 11.7 meters, and stand 5 had a mean tree height of 10.9 meters. Across all three stands tuliptree and bigtooth aspen were the tallest species present, with red maple among the tallest species in stands 4 and 5, and white ash consistently occurring at heights below the stand mean (Figure 1).

Comparisons of height-age curves across different environmental gradients revealed a consistent pattern in how species vertically stratify over time (Figure 2). Across all slope and aspect classes, bigtooth aspen and tuliptree were generally the two tallest species, with the exception of less steep slopes where red maple stems were second in height to bigtooth aspen. White oak and sugar maple stems were consistently the shortest species. White oak stems were slightly taller with age than sugar maple on xeric and steep slopes.

A comparison of canopy position of white oaks across aspect and percent slope classes revealed no significant difference in the number of white oaks occurring in the dominant and co-dominant canopy classes versus the intermediate and suppressed canopy classes (Table 3). There were 32 white oak stems that were relegated to lower canopy positions (suppressed or intermediate), and 25 stems that achieved upper canopy positions (co-dominant or dominant; Table 3). For percent slope, there were 12 stems in upper canopy positions on slopes $\geq 8\%$ and 13 stems that were on slopes $< 8\%$. Chi-squared analysis of

white oak abundance vs. slope position revealed no significant differences ($df=1$, $\chi^2 = 1.2$, critical value = 3.84, $p > 0.05$). For aspect, there were 15 white oak stems that occupied upper canopy positions on transformed aspects ranging from 0-1, and there were 10 stems that occupied upper canopy positions on transformed aspects ranging from 1.01-2. We observed 15 white oak stems in lower canopy positions on transformed aspects ranging from 0-1, and 10 stems on transformed aspects ranging from 1.01-2. Chi-squared analysis of white oak abundances vs. transformed aspect revealed that the differences observed were not greater than would be expected by chance ($df=1$, $\chi^2 = 2.2$, critical value = 3.84, $p > 0.05$).

A comparison of mean crown area of species across aspect and slope classes revealed no significant difference in the size of species crowns occurring on mesic, xeric, steep, or less steep plots (Figure 3). White oak consistently has smaller crowns than its competitors in any canopy class.

3.5 Discussion

Our results did not show significantly different abundances of white oak stems in dominant or co-dominant canopy positions on xeric aspects or steep slopes 23 years after clearcutting. However, there were more white oaks in codominant positions on aspects that were more xeric, and had percent slopes greater than 8%. This suggests that white oak dominance over time could be influenced by topography with greater growth occurring on more xeric or steep sites. The limited range of aspect and slopes across all three stands could be contributing to a lack of significance. None of the stands had transformed aspect values ≥ 1.17 , which indicates that there were no highly mesic plots. Swaim et al. (2016) also observed that slope and aspect were poor predictors of height

growth. However, Morrissey et al. (2008) noted that the competitive ability of white oak species had a strong relationship to site variables. Their study found that recurring drought events led to a reduced growth response from tuliptree, which in turn allowed oak species to establish. They also determined that xeric conditions associated with aspect allowed oak to outcompete other species vertically during drought events (Morrissey et al. 2008).

Across species, our study found that dominant and co-dominant trees had greater crown areas than intermediate or suppressed trees, although this was not statistically significant. Competition from non-white oak species was greatest in the co-dominant and intermediate canopy positions, with strong competition coming from maple and early pioneer species. Earlier research in these stands found that trees that ultimately reached the canopy were already the tallest trees six years after harvest (Swaim et al. 2016). We observed a similar trend in our data, with white oak falling behind in height growth soon after stand initiation. Therefore, post-harvest treatments to reduce the cover of these species is required to facilitate recruitment of desired species (Gingrich 1971), and should be conducted during the first 10-20 years of early post-harvest stand development (Zenner et al. 2012).

The tallest species of canopy trees we observed in our study (red maple, tuliptree, and bigtooth aspen) were also the dominant species in other studies of post-harvest stand development (Sander and Clark 1971, Heiligmann et al. 1985, Smith and Ashton 1993, Swaim et al. 2016) where pioneer species maintained dominance following clearcutting. These species were the tallest regardless of aspect and slope class. Regardless of when it established, bigtooth aspen consistently was the tallest stem across environmental

conditions, which may be attributed to its asexual reproductive abilities that allow it to maintain root reserves following disturbance (Smith 1986).

In our study, we determined that white oak was consistently among the shorter stems within the canopy, growing very closely with sugar maple. As highlighted by our height-age curves (Figure 2), growth rates of all species appeared to still be increasing (at different rates) at the time of destructive sampling. This suggests that 23 years is a long enough period for a highly productive stand to undergo canopy stratification, and that our stands were still undergoing stem exclusion (Oliver and Larson 1996). As these stands continue to develop, climatic events such as drought (Morrissey et al. 2008) and ice storms (Wonkka et al. 2013) or repeated surface fire (Hutchinson et al. 2005) could ultimately shift species composition and alter stratification patterns.

Information about how species stratify over time following harvest and other forest disturbance is an important component of effective forest management (Oliver 1978, Smith and Ashton 1993, Lockhart et al. 2006, Morrissey et al. 2008, Zenner et al. 2012, Swaim et al. 2016). Our study suggests that white oak stems are outcompeted early in the post-harvest developing stands. It would appear that none of the mechanisms that allow oak species to maintain dominance (inherently faster growth, initially superior crown position, or even persistence) contributed any advantage to white oaks following disturbance. Rather, it seems that inherent differences in species height growth, particularly the rapid early height growth exhibited by aspen and tuliptree, which are both sustained growth species, allowed these competitors to establish dominance early on and maintain their dominance 23 years following clearcutting. Differences in site quality associated with aspect and slope steepness did not appear to favor white oak dominance.

Determining patterns and trends in early stand development is crucial to make effective management decisions that maintain and create healthy and sustainable oak forests across the Central Hardwood Region. If the factors that influence canopy stratification can be discerned early on in stand development, species of high economic and ecological value can be released sooner, ensuring that these species persist over time as the new canopy layer emerges.

3.6 Tables and Figures

Table 1. All species sampled across the three stands organized by crown class and the number observed in each crown class. Canopy class codes are: D = dominant, C = co-dominant, I = intermediate, and S = suppressed. Species codes are as follows: ACRU = red maple, ACSA = sugar maple, CARY = hickory, FRAM = white ash, LITU = tulip poplar, NYSY = blackgum, OSVI = ironwood, PRSE = black cherry, POGR = bigtooth aspen, QUAL = white oak, QUCO = scarlet oak, QURU = northern red oak, QUVE = black oak, SAAL = sassafras, RHUS = sumac.

Species	Canopy class			
	D	C	I	S
QUAL	0	28	30	2
ACRU	0	13	0	0
ACSA	0	7	8	0
CARY	0	1	0	0
FAGR	0	2	0	0
FRAM	0	6	1	0
LITU	1	11	0	0
OSVI	0	2	2	0
POGR	3	4	0	0
PRSE	0	9	0	0
QUCO	0	8	0	0
QUVE	0	5	0	0
RHUS	0	2	0	0
SAAL	0	9	5	0

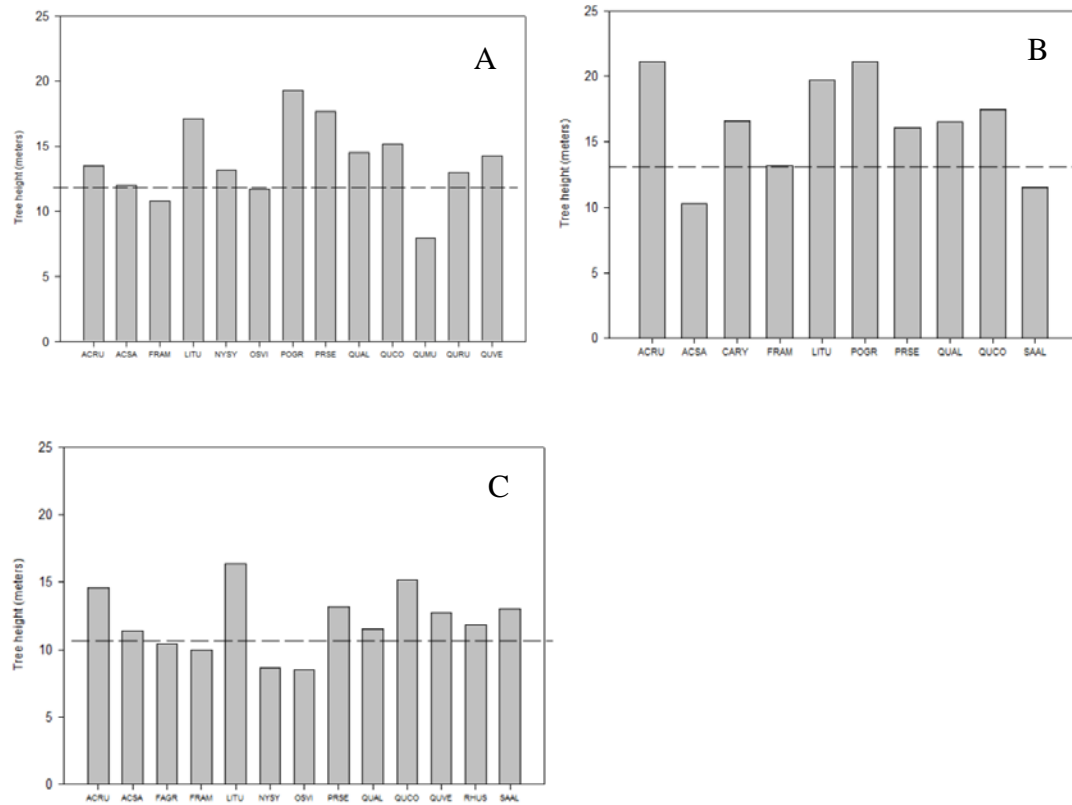


Figure 1. Height distribution of species for A) Stand 3, B) Stand 4, and C) Stand 5. The dotted line reflects mean stand height for all trees sampled within each stand.

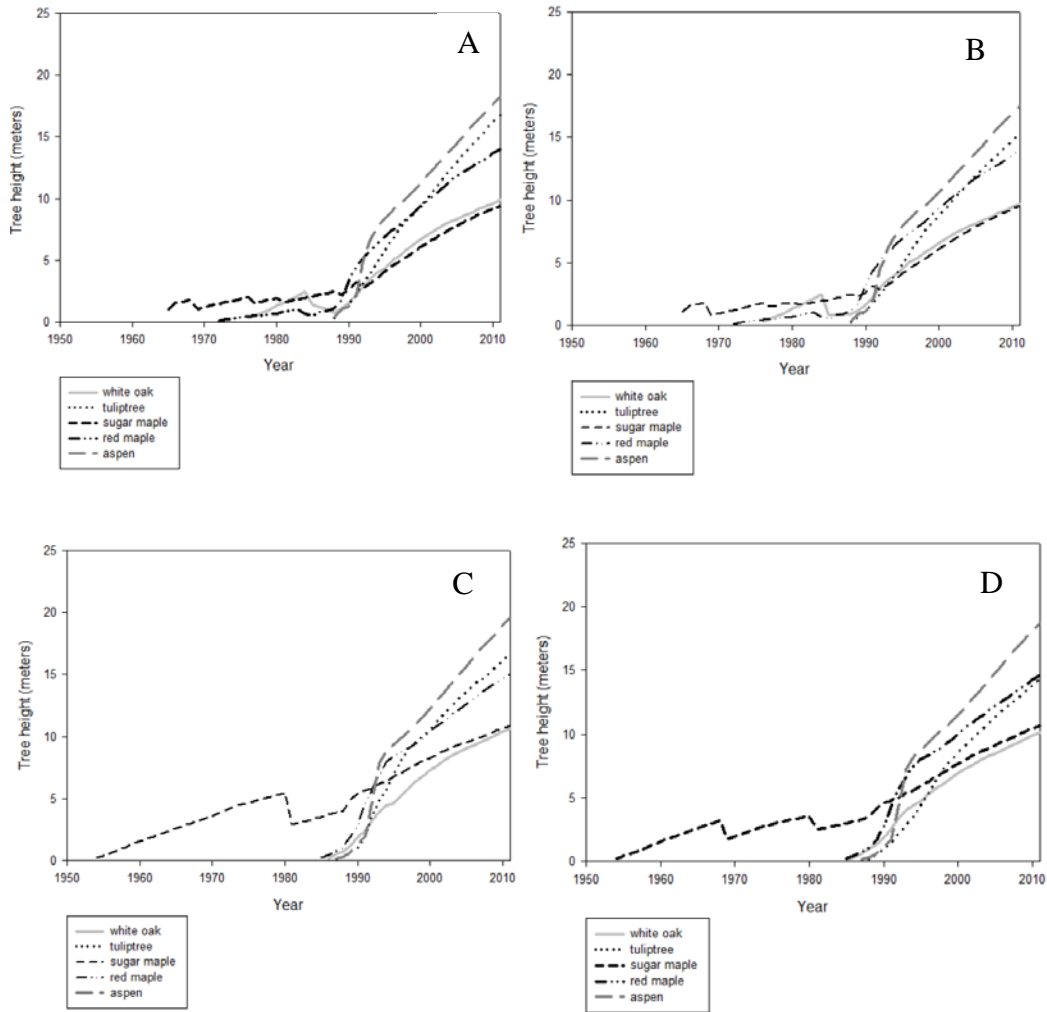


Figure 2. Mean height-age comparison of white oak to the four most abundant competitors on A) xeric, B) mesic, C) steep, D) less steep plots. Xeric values correspond to transformed aspect values ranging from 0-1, and mesic values correspond to 1.01-2. Steep plots were defined as $\geq 8\%$ slope, and less steep plots were slopes $< 8\%$.

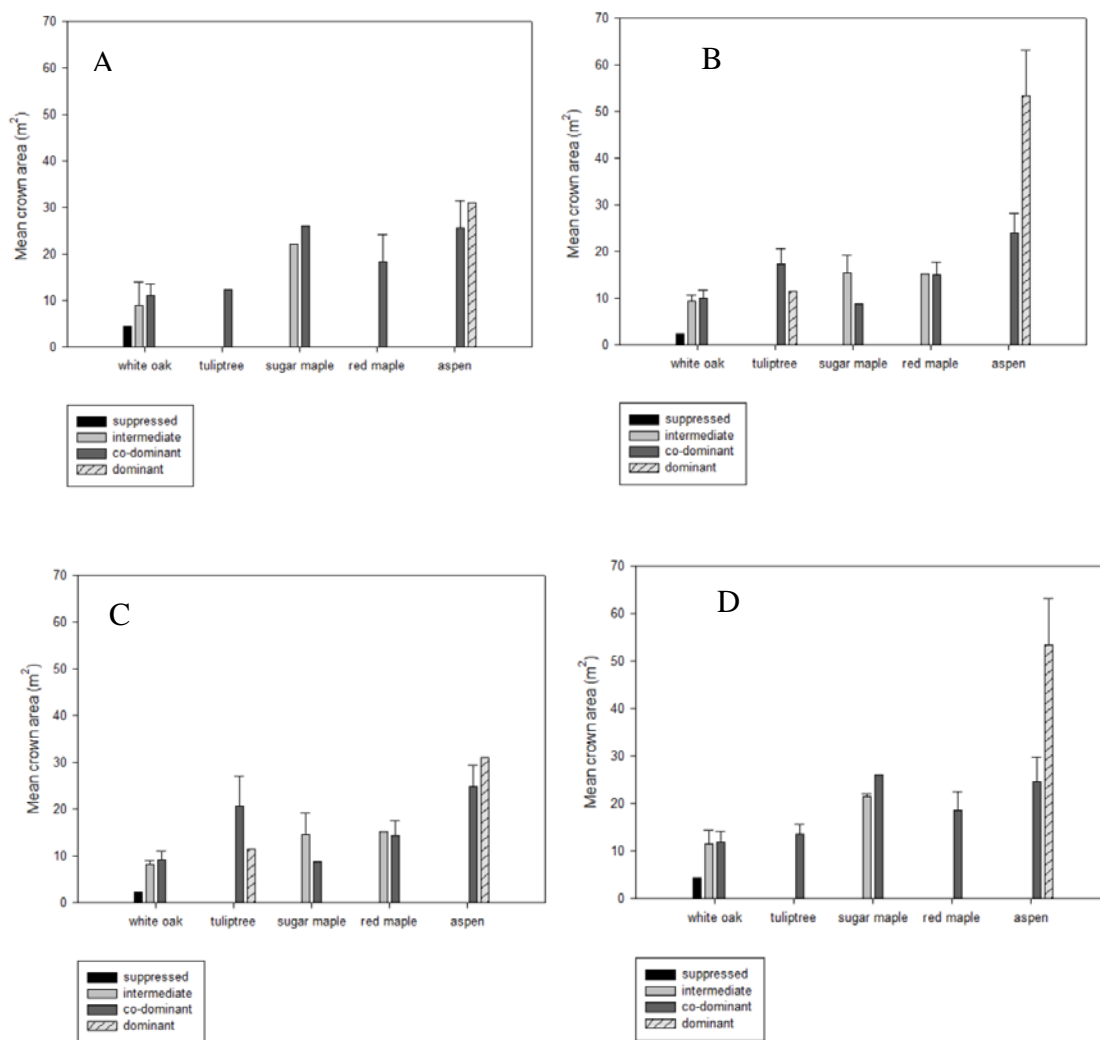


Figure 3. Mean projected crown area \pm SE by canopy position for white oak and competitors on A) mesic, B) xeric, C) steep, and D) less steep plots

Table 2. The range and mean \pm SE of site variables for each stand sampled. Aspect values reflected Beers' transformation, where values near 0 correspond to xeric environments and values near 2 correspond to mesic environments.

stand	Size (ha)	aspect			percent slope		
		min	max	mean \pm SE	min	max	mean \pm SE
3	8.1	0	0.91	0.29 ± 0.07	1	18	7.88 ± 1.08
4	7.6	0	1.5	0.89 ± 0.10	1	11	7.52 ± 0.50
5	4.5	0.06	1.17	0.55 ± 0.08	5	10	7.7 ± 0.33

Table 3. Chi-square analysis for canopy position of white oak vs. aspect and white oak vs. percent slope across each stand sampled. Canopy was organized into four classes: 1) dominant, 2) co-dominant, 3) intermediate, and 4) suppressed. Aspect was divided into two categories: 0-1, and 1.01-2. Percent slope was also divided into two categories: $\geq 8\%$ and $< 8\%$.

Oaks by canopy position	Beers' Aspect		Percent Slope	
	0-1	1.01-2	$\geq 8\%$	$< 8\%$
white oaks (1-2)	25	7	20	12
white oaks (3-4)	15	10	12	13
Chi-square (χ^2)		2.2		1.2
Critical value				3.84
P < 0.05	3.84			NO
		NO		

CHAPTER 4. CONCLUSIONS

Environmental differences between sites in Missouri and Indiana reflect innate differences in species competition and in turn offer different potential management scenarios for each respective site. In Indiana, a narrower range of environmental variables were measured than in Missouri. This likely contributed to the inability to detect strong environmental influences at the Indiana sites, whereas in Missouri oak species displayed a stronger relationship with environmental variables, in particular a stronger affinity with more xeric aspects and convex topography. The density of advance regeneration of the white oak species group was greater at the Indiana sites, while the red oak group was greater in density at the Missouri sites. The composition of competing non-oak species differed between sites, but occurred within the same 5-25 cm diameter range at both sites. In Indiana, non-oak competition in this diameter range was primarily maple species, whereas in Missouri flowering dogwood and blackgum were the most abundant competitors.

Stratification patterns 23 years following clearcutting displayed no major differences regardless of aspect and slope steepness. Comparisons across these different gradients revealed that early successional species consistently were the tallest species, with white oak was relegated early on to lower positions where it grew very closely with sugar

maple. A closer look into the stratification patterns on a case by case level revealed two noticeable trends. First, in similar fashion to Oliver (1978) who studied the stratification patterns of red oak in mixed species forests of the New England, all white oaks in Indiana that were winners at the time of sampling were smaller in height than their competitors at the time of establishment. This could potentially be due to persistence, where the oak species is able to maintain itself for a long enough period of time until it's competitor faces some type of physical or environmental stress that reduces its growing ability and eventually allows the white oak to surpass it. The second observed trend occurring in only a few cases was a noticeable inflection point where competitor's height growth halted and became negative, which corresponded to the presence of the second competitor establishing within a plot. White oaks were then able to surpass competitors at this time. This type of inter-tree competition has been suggested before in silviculture through the use of trainer trees (Smith et al. 1986), and could reflect the differences in species success associated with spacing as discussed in Oliver and Larson (1996) and Lockhart et al. (2006).

When considering how to move forward with management of the sites from the southern portion of the Hoosier National Forest, we suggest the use of vegetative control techniques that are similar to those recommended by Loftis (1990) or Lorimer (1994), such as mechanical and chemical treatments to reduce vegetative competition (particularly maple species, aspen, and tuliptree) in the understory layer in order to facilitate oak regeneration. This recommendation is based on our observations that these species establish early in stand development, and are immediately able to surpass oak species in height growth and stem density. Therefore these pre-harvest site preparation

techniques should produce adequate growing space to recruit oak advance regeneration with the intent on producing larger root collar diameters that would give oaks more resources to respond aggressively to future disturbances. Methods involving fire may not initially be as effective; because of the considerable density of species in the midstory layer (white ash, maples, ironwood, and greenbrier), existing oaks will have depleted nutrient stores to respond to fire and it may be difficult to carry fire with the low flammability fuel beds these species produce. Use of fire therefore should be withheld until a later point in time when more oaks have established in the understory layer after mechanical or chemical treatments. However, site prep burns (Brose et al. 2013) could potentially be used to reduce competition from non-oak species by reducing leaf litter densities and reducing the presence of competitor species within the seed bank.

Stand structure of these site in the southern portion of the Hoosier National Forest suggest that harvest entries should occur within the next few years. Our results indicated a slightly binomial diameter distribution, where trees ranging from 25 -40 DBH cm were roughly as abundant as trees that were 15 cm DBH, suggesting that the appropriate time to begin some type of even aged management would be now. Removal of the larger diameter trees is not recommended at this time, with the exception given to economic requirements associated with logging contracts. The focus of removal should be mostly on the tree 10 – 25 cm DBH because stems in this size class occur in high densities that will compete with advance regeneration. This removal would create a zone of high shade that favors oak species development over their competitors such as tuliptree; which generally have a higher light requirement (Loftis 1990). Special attention should be given to the red oak species present on site. Red oak stems are not nearly as abundant as those

of white oak, especially in the larger size classes. If recruitment of red oak is to continue on these sites then additional consideration will have to be given to seed source and spacing.

Management recommendations for the Missouri sites does not pose the same complexities as those for the Indiana sites. , For stems greater than 25 cm DBH in Missouri we observed a substantial shift in composition from white oak species to red oak species. As pointed out by Johnson et al. (2009), white oak is moderately tolerant of shade and less tolerant of drought, so when high intensity light conditions coincide with drought as is common in Missouri, dominance by red oak group species (black and scarlet oak) may be favored in these larger diameter classes. The structure of stands at our sites in Missouri follows the reverse-J shaped distribution associated with even aged stratified mixtures (Smith et al. 1986). This likely due to even-aged management practices already taking place on the sites (Kabrick et al. 2014).

Fire offers a viable management option for future oak recruitment in Missouri. Within the midstory layer, white oak maintained dominance in the 10-20 cm diameter size class. Competition between white oaks and other vegetation was greatest at the 5 cm DBH diameter class (Quackenbush et al. 2016), with the majority of competition coming from black gum and flowering dogwood. Using the Brose et al. (1999) shelterwood burning method could prove more beneficial at this sites than the use of chemical and mechanical treatments, especially since the use of repeated burning has been shown to reduce the seed source of non-oak competition and favor oak species in early stand development in similar forests (Dey and Hartman 2005, Johnson et al. 2009).

When comparing the Indiana and Missouri sites, one of the most noticeable differences is the abundance of maple species. Missouri sites had few or no maple species across diameter classes while sites in Indiana contained a rather large abundance of maple species, most noticeably in the 5-15 cm DBH diameter range. This size range is an important reservoir for future overstory recruitment, as these are the trees that will eventually become the new canopy over the course of forest development. Without management intervention maple species and ironwood will continue to occupy the smaller diameter classes, preventing oak recruitment into the canopy at the Indiana site. Environmental variables, particularly aspect, were discovered to be correlated with the separation of species and plots between Missouri and Indiana (Chapter 2, Figure 2). Within the Missouri site, we observed the greatest density of black oak advanced regeneration occurred on xeric aspects with convex topography. The environmental influences associated with aspect may also explain the stark contrast in the amount of red oak species vs. white oak species advance regeneration between the two sites. In Missouri, where there was a greater range of aspects and topography, there was a greater density of red oak species present in the smallest diameter class (0-5 cm DBH), but in Indiana where there was a narrower range of aspect and topography which were primarily mesic in nature, white oaks were more abundant than red oak species in the smallest diameter class (0-5 cm DBH). This association between xeric topography and red oak group species was also observed by Nowacki and Abrams (2008).

In closing, our study illustrates the importance of pre-harvest data in developing management prescriptions. Knowing how environmental variables influence the distribution and composition of advance regeneration provide critical insight in to how

and why a particular forest stand should be managed. Our study also illustrates that the winner and losers in post-harvest stands are determined early in stand development. This information provides a basis for making informed decisions based on empirical evidence and contributes to a growing body of literature concerned with maintaining the health and quality of our eastern hardwoods forests.

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